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CYTOLOGY, HOMOLOGY AND PHYLOGENY—A NOTE ON "ORGANIC DESIGN"

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The diversity in form and function of living organisms, great as it is, is not infinite. At all levels of organization, from single enzymes to the most complex organ-systems of the higher Metazoa, there may be more or less pronounced resemblances between different organisms. Although the problem currently receives little attention, the explanation of the origin of these resemblances still constitutes one of the more important general biological themes. In making a distinction between *homology* and *analogy*, comparative anatomists long ago recognized that morphological resemblances between organisms may be of two kinds. According to current usage, homology implies the existence of precise morphological similarities between the parts of organisms which, being built on the same structural plan, are considered to be phylogenetically related through a common ancestor. Analogy, on the other hand, denotes the occurrence of structural resemblances between organs of similar function, regardless of phylogenetic relationships. The aim of this paper is to draw attention to the necessity of making this distinction not only in comparative anatomy but at all levels of organization. In particular it is proposed to examine the difficulties which arise in attempting to do this at the lower levels. The viewpoint adopted is by no means new and, indeed, has recently been most persuasively argued by Pantin (1951). The only excuse for its reiteration here is that it still appears to be insufficiently appreciated, especially by cytologists and by those who concern themselves with the phylogeny of the lower organisms.

COMMON ANCESTRY VS. INDEPENDENT ORIGIN

We may begin by considering two examples at opposite ends of the scale of biological complexity. Reptiles, birds and mammals all possess pentadactyl limbs; platyhelminthes, lamellibranchs and insects all use quinone-tanned proteins as structural materials. It seems that these two sets of resemblances must receive different interpretations. In the first case the structures are so complex and improbable and the organisms so obviously closely related that, even without paleontological evidence, we could be virtually certain that the resemblances are correctly interpreted in classical

terms, by postulating common ancestry and hereditary transmission of the ability to produce the structures in question. In the second case, however, the organisms do not appear to be closely related and the character in which they resemble each other is of a relatively low order of complexity, so that explanation in terms of common ancestry seems improbable. It appears far more likely, as Pantin (1951) suggests, that, given the existing biochemical basis of life, the use of a quinone-tanned protein is one of the few possible solutions to the problem of producing a material with the required structural and mechanical properties. If this is so, we may expect to find that the same solution has been reached independently in more or less unrelated organisms.

These two examples are extreme cases, in which it is virtually certain that the two explanations (that is, common ancestry and independent origin, respectively) are correct. Between these extremes of simplicity and complexity there exists a great range of structural and physiological resemblances to which one or other interpretation can be applied with greater or less certainty. We may take as an intermediate example the striking similarities of the early embryonic forms of a whole range of Metazoa. In the heyday of the Biogenetic Law such resemblances were confidently taken as evidence of common ancestry, but perhaps we should now be more inclined to agree with Oskar Hertwig's view:

> . . . it cannot surprise us that in all animal phyla the earliest embryonic processes take place in similar fashion, so that we observe the occurrence both in Vertebrates and Invertebrates of a segmentation-process, a morula-stage, a blastula and a gastrula. If now these developmental processes do not depend on chance but are rooted in the nature of the animal cell itself, we have no reason for inferring from the occurrence of a similar segmentation-process, morula, blastula, and gastrula in all classes of the animal kingdom the common descent of all animals from one blastula-like or gastrula-like ancestral form.
>
> The principal reason why certain stages recur in ontogeny with such constancy and always in essentially the same manner is that they provide under all circumstances the necessary pre-conditions through which alone the later and higher stages of ontogeny can be realised. The unicellular organism can by its very nature transform itself into a multicellular organism only by the method of cell division. Hence, in all Metazoa, ontogeny must start with a segmentation-process and a similar statement could be made with regard to all later stages.
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> (Quoted from Russell, 1916, pp. 354-355.)

In other words, blastulae or gastrulae should be regarded as *necessary* stages of all higher multicellular organisms, as forms which, determined primarily by functional and morphogenetic requirements, may have arisen independently on numerous occasions and therefore cannot be taken as unequivocal evidence of common ancestry. All sexually reproducing Metazoa, starting life as fertilized eggs, face essentially the same problem—a single cell must be converted into a complex, highly differentiated, multicellular organism. The number of properties and processes which are available for carrying out this task is strictly limited. Eggs can divide; after division, the cells can change shape; they can adhere or fail to adhere, they can in-

teract in induction processes, become biochemically differentiated, and so on. These processes we may expect to find at work in all embryos, and given such basic potentialities, and a common developmental problem, there must inevitably be similarities in the ontogeny of all Metazoa and a recurrence of the same basic morphological forms. This viewpoint, if not capable of direct proof, certainly cannot be refuted by any evidence at present available. If it be doubted whether convergence alone can produce such precise similarities in embryonic forms, we need only refer to the extraordinary parallels which have arisen in this manner between two far more complex structures—the eyes of cephalopods and vertebrates.

The same arguments can be applied, but with even greater force, at the lower level of organization represented by cells and their constituent organelles. One of the most striking facts which the electron microscope has so far revealed is the remarkably constant and uniform structure, through a wide range of material, of such organelles as cilia and flagella, mitochondria, nuclear membranes and the Golgi apparatus. The latter, for example, contains as a characteristic component a pile of flattened sacs (that is, a stack of membranes joined at their edges in pairs). These have now been demonstrated in somatic and germinal cells of vertebrates (Sjöstrand and Hanzon, 1954; Dalton and Felix, 1954) and invertebrates (Afzelius, 1956; Grassé et al., 1956; Lacy and Horne, 1956; Dalton and Felix, 1956), in zooflagellates (Grassé and Carasso, 1957; Grimstone, 1959), phytoflagellates (Sager and Palade, 1957; Rouiller and Fauré-Fremiet, 1958) and higher plants (Lance, 1957; Buvat, 1957). The equally constant basic structure of the other organelles could be similarly documented.

The suggestion that these organelles, in spite of their great similarities, could have arisen independently, seems plausible, even though, as with the embryonic forms, it can scarcely be proved. It is possible, for example, that the constant structure of cilia and flagella throughout the plant and animal kingdoms indicates that this particular arrangement of fibers is the only possible method—possible, that is, to living organisms as we know them—of constructing an organelle with the required mechanical properties. Consequently, it could have been arrived at independently by different groups of organisms. Similarly, the characteristic structure of mitochondria may well be the only solution to the problem of organizing enzyme systems on surfaces, while at the same time providing adequate access to substrates, etc., and the closed sacs of the Golgi apparatus, in which bulky secretory products seem to accumulate, may represent the only possible method of constructing a secretory organelle. The hypothesis of independent origin, while admittedly more open to question in these examples than at the biochemical level (exemplified by the quinone-tanned proteins discussed above), must at present still be regarded as a very distinct possibility.

Pantin (1951) has pointed out that one of the reasons why we must expect organisms to arrive independently at the same solutions to common functional problems is that the number of *possible* answers is severely restricted

by limitations in the number and kind of the parts and properties available in nature. It is becoming steadily clearer, for example, that at the fine-structural level the basic components of cells—membranes, fibers, granules —are few in number. Given the existing biochemical basis of life, these are the building units from which cells must be constructed, and it may reasonably be supposed that the number of ways in which they can be put together to form a functioning cell is subject to stringent limitations. Evolution appears to have little room in which to maneuver at this level. The very fact that we know of no analogue of Golgi apparatus or cilium could well be taken as an indication that they are the only possible solutions to given functional problems. It must also be remembered that the properties of the inanimate world—surface tension, for example, or the forces of inter-atomic and inter-molecular attraction generally—which impinge equally upon all organisms, play a much greater role in shaping structure at the cellular and sub-cellular levels than in structures of a higher grade of organization.

The 'common biochemical basis of life,' which has been referred to above, is itself not necessarily to be explained in terms of common ancestry; the arguments advanced long ago by Henderson (1913) still retain their validity. Given the existing physical and chemical properties of the elements and their compounds, only one sort of life appears to be possible; providing we do not suppose the origin of life to have depended upon a series of extremely improbable events, there is at present no compelling reason for believing that all living organisms derive from a single starting point.

GENETIC CONSIDERATIONS

To clarify the argument, and perhaps prevent confusion, it is now proposed to remark briefly on certain genetic aspects of the problem.

To begin with, it might be objected that the distinction made between different characters on the basis of their level of complexity is a spurious one. In view of the known divergent nature of developmental processes, it might be postulated, for example, that the genetic determinants of a pentadactyl limb are not necessarily more complex than those of a set of Golgi membranes, and, if this were the case, the probability of independent origin of the two would be the same. This, however, is obviously incorrect. To take two extreme examples again, the production of the globin moiety of hemoglobin (an example of a low-order, biochemical characteristic) is known to depend on only a single gene (Ingram, 1957); the vertebrate limb, on the other hand, is undoubtedly determined by a great many, for at least a dozen genes are known to affect limb development in the mouse alone (Grüneberg, 1952) and a similar situation exists in other vertebrates (see Needham, 1942). In discussing different levels of organization we can therefore assume that the complexity of the end-product is roughly paralleled by that of its genetic determinants.

Secondly, it must be made clear that whether characters are thought to have arisen once or many times, there is no reason to suppose that there are any fundamental differences in the evolutionary mechanisms at work. In

both instances we may make the orthodox assumption that natural selection works on whatever variations the organism may present.

Thirdly, while it is suggested that structures such as cell organelles may have evolved independently in different groups of plants and animals, it is not questioned that, once acquired, these structures (or the potentiality to produce them) can be handed on from one generation to another. This, however, is far from proving that they have been evolved only once. There may well be genetic continuity of the Golgi apparatus within a group such as the zooflagellates, but the assumption that the organelle in one of these organisms is genetically continuous with that in, say, an invertebrate spermatid, may well be quite unjustified, even though the two organelles may be morphologically almost indistinguishable. The essential point is that structures of low complexity, dependent, as it seems, on a small number of genes, could have evolved many times, in contrast to the more complex and improbable Metazoan organs which, determined by a far more numerous set of genes, appear to have arisen only once.

HOMOLOGY

It is appropriate now to consider the manner in which the term *homology* should be defined in the light of the above discussion. For the pre-Darwinian comparative anatomists, such as Owen, structures were homologous which were morphologically similar and which occupied corresponding positions in two organisms built on the same structural plan. (For the history of the homology concept see the admirable reviews of Russell, 1916, and Spemann, 1915.) If this meaning be adhered to, there is no objection to its application to the parts of embryos and to cell organelles, for the definition is free of any hypothesis as to the origin of the similarities. As is well known, however, the advent of Darwinism brought about a change in meaning of the term, for since organisms built on the same structural plan were now thought to be evolutionarily related, any structure which they possessed in common must be derived from a structure present in a common ancestor. This, from being an explanation of homologies, rapidly became a supposed criterion: "The sole criterion which organs must fulfil to be homologous is to be descended from one and the same representative in a common ancestor." (de Beer, 1928.)

Using the methods of symbolic logic, Woodger (1945) demonstrated rigorously that in fact the evolutionary criterion of homology is illogical: phylogenetic relationships are postulated on the basis of morphological similarities, not *vice versa*. The resemblances detected by comparative anatomists and which we now call homologies may indeed be correctly explained in evolutionary terms, but this is irrelevant to their initial recognition. Strictly, therefore, the term homology should be used only in its pre-Darwinian sense.

However, logical or not, the evolutionary definition of the term is undoubtedly still the most popular. Simpson (1958, p. 533) states that, "By widely accepted definition homology is resemblance due to inheritance from a common ancestry," adding, in a footnote, that in a recent "flare-up of

highly polemic discussion" of the definition of the term, "A group that insisted that 'homology' should not imply community of inheritance was definitely in the minority." It therefore appears that if we describe parts of cells as homologous, the majority of biologists will understand us to imply that we consider these parts to be derived from the same structure in a common ancestor. This, of course, is precisely the implication we ought to avoid.

In practice, cytologists usually use the word homology without giving any clear indication of what they understand by the term (see, for example, Grassé and Carasso, 1957; Dalton and Felix, 1957; Baker, 1958). Sometimes, however, they adopt the evolutionary definition (Gatenby, Dalton and Felix, 1955) and occasionally they use the word in both senses at once, which may lead to confusion. As an instance of the latter we may quote from a paper of Pitelka and Schooley (1955). After describing the mastigonemes (lateral appendages) on a variety of Protistan flagella, they write:

> Perhaps the first question to consider is whether the structures that we have been calling mastigonemes are indeed homologous in the various groups. We believe that they must be so. Certainly their differentiation into base and terminal filament in all groups studied argues for a basic structural relationship. If they are homologous, their presence must have a common functional explanation in all groups.

This statement is followed by a discussion of the value of mastigonemes as taxonomic characters, in which, in spite of inconsistencies in the distribution of these organelles in different groups of Protista, their taxonomic usefulness is not seriously questioned. It is clear that the two meanings have become mixed here. It is first asserted that, since mastigonemes are similar in structure, they must be homologous; in other words, this is a pre-Darwinian usage of the term. From this, however, Pitelka and Schooley go on to use the mastigonemes in taxonomy, which is only permissible if they are homologous in the evolutionary sense. The last sentence quoted is a *non sequitur* (for we are never entitled to deduce similarity in function from the existence of homology, whether the latter term is used in its pre- *or* post-Darwinian sense) but nevertheless seems to contain a recognition of the fact that morphologically similar structures can arise in response to common functional needs. With this we may agree. It seems highly probable that in fact mastigonemes have arisen independently in several groups of Protista, perhaps in response to a common need to increase the effective surface area of flagella, in which case they are homologous only in the pre-Darwinian sense and are valueless as taxonomic characters. To avoid such confusion it would be advisable either to avoid the term homology altogether in cytological contexts or else use it only with careful specification of the sense in which it is employed.

In comparative anatomy the concept of homology has always been closely bound up with the idea of the *archetype*; that is, the hypothetical, generalized organism from which existing forms could in principle be derived. The concept has been of considerable importance: Goethe sought (and found) the

intermaxillary bones of man, "only because he was firmly convinced that the skeleton in all higher animals was built upon one common plan and that accordingly bones such as the intermaxillaries found well developed in some animals, must also be found in man." (Russell, 1916, p. 46.) Not unexpectedly, the idea has been taken over, consciously or unconsciously, by cytologists, who not infrequently appear to think in terms of an archetypal cell, all the parts of which are necessarily represented in all (or most) existing cells. It must surely have been this idea which inspired the repeated efforts to discover the Golgi apparatus in ciliates and other Protozoa (see Smyth, 1944) and which led to the homologizing of Golgi apparatus and contractile vacuole, even when there was little more on which to base the homology than a common ability of the two structures to reduce osmium tetroxide. It may indeed be true, as has recently been claimed (Gatenby, Dalton and Felix, 1955), that electron microscopy shows the walls of the contractile vacuole to be similar in fine structure to the Golgi apparatus, though the evidence presented for this so far is not entirely convincing. However, this is unimportant here; the essential point is that the cell should not be thought of in terms of concepts which properly belong to an altogether different level of organization. If Golgi apparatus and contractile vacuole are similar in fine structure it is surely at least as probable that the resemblance arises from the fact that they are in some way similar in function, as that they are both derived from the same ancestral, ever-present organelle. In brief, the concept of the archetype can never be for the cytologist or protozoologist what it was for Goethe, a guiding principle on which to base the search for structures.

PHYLOGENY

Finally, it may be useful to indicate briefly the implications of the ideas presented here for discussions of the phylogeny of the lower organisms, and in particular of the origin of the Metazoa. These are matters in which there has recently been a certain revival of interest (see, for example, Hardy, 1953; Carter, 1954; Fauré-Fremiet, 1958; Hanson, 1958). The implications should be clear: attempts to trace evolutionary pathways at that level generally involve the comparison of organisms, or parts of organisms, to which the concept of homology can only safely be applied in its pre-Darwinian sense. Resemblances are likely to be the result of convergence.

Hanson (1958) has recently made detailed comparisons of ciliates and the Acoela in an attempt to provide stronger evidence for Hadzi's view that the former may have given rise to the latter and thus initiated the Metazoa. It may indeed be true that the cellularization of a protozoon is the more probable method by which the Metazoa arose, but unfortunately, in comparing the Acoela and the ciliates Hanson makes little attempt to distinguish between characters which might conceivably be useful as phylogenetic indicators and those which probably result from convergence. It could be argued that there is scarcely a point of similarity between the two groups which could

not fall into the latter class. It goes almost without saying that this is true of such features as ecology, ethology, comparative physiology and biochemistry, but it is also true of morphology and life cycles, on which the proposed phylogeny is chiefly based. For example, the Acoela, like certain ciliates, tend to be bottom-living forms feeding on small plants and animals. The two are about the same size and appear to occupy approximately the same ecological niche; similarities in morphology are therefore not unexpected. Movement by cilia, found in both groups, is a common feature of organisms of that size and habit, and the apparently similar fiber systems linking the basal granules of the cilia are surely to be expected on functional grounds. Similarly, the multinucleate condition, as Hanson himself suggests for the Foraminifera, could well be an adaptation to cope with increased cytoplasmic volume, and therefore likely to appear in many organisms. Possibilities such as these should surely cause one to be somewhat hesitant about postulating an evolutionary relationship between the two groups. It is true that the existence of many points of similarity increases the likelihood of a phylogenetic relationship, but it must be remembered that the evolutionary adaptation of an organism to a certain environment and mode of life involves a whole plexus of *inter-related* characters, the existence of one of which presupposes that of the others.

Fauré-Fremiet (1958) draws attention to the remarkable similarity in fine structure between the photoreceptors of vertebrates and those of the phytoflagellate, Chromulina. He suggests, though with the greatest caution, that this might provide support for the view that the Metazoa arose from the Metaphyta. Here again, however, the resemblance is probably to be explained at least as plausibly by postulating independent origin as by invoking common ancestry.

It is by no means suggested here that the functional interpretation of the resemblances between lower organisms is necessarily always the correct one, but it is surely sufficiently likely to deserve far more attention than it usually receives in phylogenetic discussions. It is indeed arguable that at the present time we might more usefully content ourselves with speculating on the nature of the processes which have gone on in the evolution of the lower organisms, rather than attempting to trace detailed phylogenies. For example, it is still useful to enquire whether the Metazoa arose from a colony of Protozoa or from a single individual, or, at a lower level, to try to envisage how a bacterium could be converted into a higher type of cell, even if with existing methods we cannot hope to discover the precise phylogenetic pathways along which these changes occurred.

SUMMARY

The origins of the resemblances between living organisms are discussed. It is suggested that at the lower levels of organization, exemplified by biochemical characters, cell organelles, and early embryonic forms, similarities do not necessarily imply common ancestry; independent origin is equally probable. The reasons for advocating this view are given and the problems

which it raises in attempting to define the term 'homology' are examined. The relevance of the idea to discussions of the phylogeny of the lower organisms is briefly considered.

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SOME ECOLOGICAL FACTORS BEARING ON THE ORIGIN AND EVOLUTION OF PIGMENT IN THE HUMAN SKIN

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It is generally assumed that most morphological and physiological characteristics either have or have had significant adaptive value and hence have contributed to their possessors' survival. This assumption includes both internal and external traits and on this basis it seems legitimate to assume that in man as in the majority of other terrestrial vertebrates, the nature and color of body surfaces, whether naked skin, pelage or plumage, probably represents past or current attributes that have contributed to survival.

Because vascularized naked skin comes into direct contact with the environment, differences in the dermal color of naked animals including man have usually been interpreted as having value in terms of possible physiological effects, whereas in the coloration of birds and mammals they are more frequently related to concealment in a variegated environment.

LONG AND SHORT WAVE RADIATION VS. COLOR

In man the general darkening of pigmental gradient displayed by successive populations from northern Europe southward to equatorial Africa, supplemented by the erroneous notion that temperature and radiation extremes increase continually up to the equator, has apparently implanted the vague belief that increasing pigmentation must in some manner contribute to protection against over-heating or radiation damage. Despite lack of convincing evidence for this belief, there has been stubborn persistence in retaining it. Apparently there has been a universal uncritical extrapolation from visual responses to differences in the coefficient of reflection (hereafter called the *albedo*) to include the invisible radiation in the infrared and ultraviolet, even though it is well known that what is seen by the human eye cannot provide information on the functioning of these invisible rays. Similarly, although the facts are widely known, the actual thermal blandness of equatorial climates is usually ignored. Temperatures of 27°–30°C (78°–86°F) prevail and would be comfortable except for the very high relative humidity. By preventing an adequate evaporative rate this humidity so seriously impairs man's chief means for dissipating the body's heat load that it creates an overwhelming impression of great environmental heat. Very much higher actual temperatures are encountered in deserts where heat maxima may exceed by as much as 25°F the maxima of the equatorial regions, and radiation intensities are also greater.

In the infrared the heavily pigmented Negro skin radiates no better than a white surface (Laurens, 1933, p. 123), hence in areas of high humidity and inadequate evaporation even a black skin has no thermal advantage. If we

could see only in the infrared there would be no difference in hue between the Negro and his white-skinned counterpart.

The putative value of protection against ultraviolet by possession of a heavily pigmented skin is not supported by the facts. Primary defense against erythema and its occasional sequel of dermal carcinoma is predominantly concentrated in the overlying stratum corneum (Blum, 1945). It is the adaptive response of thickening corneal material under ultraviolet radiation that confers the predominant and possibly all but marginal protection against damage (Blum, 1945; Hall, 1950; Hardy and Muschenheim, 1934).

In any event, skin carcinoma is not an inevitable sequel to sunburn even in those that are radiation-sensitive, and in those instances where it does occur, death usually comes so late in an individual's reproductive life that it is difficult to concur with the assumption that it would constitute an effective barrier to genetic survival. Additionally, the notably short life span of primitive people would greatly minimize any purported selective value resulting from ultraviolet radiation resistance.

From these studies it is impossible to draw any conclusion other than that heavy pigmentation in the skin serves no decisively useful purpose in the conventional context. Furthermore, because about 50 per cent of the incoming solar energy reaching ground level is in the visible spectrum, and because the nearly black skin of a Negro will absorb 84 per cent of this energy (a white skin, 55 per cent) and convert it into heat in any hot sunny environment, the Negro actually accumulates a larger burden of external heat than would an equivalent white man. The actual fact seems to be that the black man has survived in genuinely hot regions not because of his heavy pigmentation but despite it.

THE VISIBLE SPECTRUM AND PIGMENTATION

If we can attribute no physiological advantages to heavy pigmentation in the invisible wave lengths, it certainly would seem reasonable to confine our speculations to the possible effects of what we can see. That we have made so little progress in discovering the function of skin albedos, in part may be attributable to insistence upon the functions of the invisible while basing the studies on criteria that are valid only in the visible light.

If it is remembered that with increasing melanization our visual cues inform us only on degrees of absorption in the visible wavelengths and that blackness does not provide any reliable information on either the absorptive or radiative efficiency in the invisible wavelengths (except in the physicists' conceptual model) it should be possible to come closer to the probable explanation of variations in albedo than we have heretofore.

Preoccupation with the physiological aspect of dermal color has been reinforced by acceptance of the so-called Gloger's principle which, with very rare exceptions, has been accepted as establishing a connection between degree of melanization in animals and some form of physiological-climatic adaptation.

GLOGER'S PRINCIPLE

Gloger (1833) (see also Allee and Schmidt, 1951; Allee, et al., 1949) was the first to report the general trend in degree of color saturation that characterizes a cline of closely related species or forms which are distributed from warm moist climates where the animals are very dark to the notably pallid occupants of cool, dry climates. The rule is equally applicable to clines extending from hot dry climates to cool damp ones, as from the California deserts to the cool wet Pacific northwest.

Because of the emphasis on physiological explanations, it has been inferred that these changes mediate thermal difficulties by adsorption of heat in an otherwise cold- or heat-extracting environment or conversely reflection of energy in an environment having superfluous heat. This thinking has been adopted in either direction as circumstances seemed to warrant, and with total disregard of the fact that in many areas the inevitable seasonal change from hot and dry to cold and wet would seem to cancel the putative advantages for any animals with more than a very brief life cycle.

When Gloger's "principle" is examined from the evidence provided by contrasting the heat sources of the ectotherms (coldbloods) and endotherms (warmbloods) (Cowles, 1950, 1958), it appears to be virtually impossible to reconcile the obvious contradictions. One group is heated effectively solely from outside, the other from within, hence the sources of heat are in 180° opposition to each other and require opposite adaptive albedos (great reflectance equal to white, absorption equal to black); hence conformity to the functions that have been inferred from Gloger's statement would be impossible for both. In addition, irrespective of the source of body heat and the reversal of the heat problems for these oppositely heated types, they both conform to the rule insofar as albedo is concerned. This being the situation, some entirely different and, in terms of their hue, some non-physiological explanation should be sought. This dilemma becomes even more apparent when we seek to explain why it is that the sedentary occupants of black lava beds lying in the hottest regions of the world, regardless of their heat source, broadly conform to Gloger's "principle" (Cowles, 1958), whereas those that live on highly reflective soil only a few feet or yards away are characteristically pallid.

The antiquity of the lava and the degree of its occupants' sedentary behavior, together with an animal's susceptibility to predation rather than some dominating physiological adaptations, appear to be the deciding factors producing their conformity to the albedo of their environment. This does not imply, however, that differences in albedo and attendant variation in rate of adsorption of energy in the visible spectrum may not have ecological significance.

It may be useful to point out that wherever Gloger's principle is applicable, the dark animals exist either where their habitat is black or very dark, or where the incident illumination is greatly reduced by the cloudiness that accompanies heavy precipitation. Furthermore, this darkness is accentuated

by the shade under the inevitable lush growth of vegetation. Darkness is additionally accentuated by damp humus on the ground surface. Wherever the animals are light in hue so is their environment, and also there is abundant illumination.

Gloger's principle should probably be restated to read: in the majority of terrestrial animals there will be a general conformity between their albedo and that of their environment, the degree of conformity being modified by need for concealment. Arboreal, subterranean and mimetic forms and those with warming coloration should represent exceptions to this general trend.

If neither a strictly physiological analysis of the problem of human skin color nor the associated inferences based on Gloger are acceptable in terms of climate, it seems reasonable to test the field naturalists' views on reduced detectability (visibility), concealing or cryptic coloration, and natural selection.

CONCEALING COLORATION

The elaborate patterns and other artifices for concealment in nature have been abundantly discussed since Darwin and recently summarized by Cott (1940). If human skin color had been determined in the same manner and by the same environmental pressures as other animals we could legitimately expect some populations to display blotched or striped patterns, and if a quadruped, man should be countershaded as well and in much the same manner as most quadrupeds having concealing coloration. All of these patterns reduce the visibility of their possessor while in his natural environment and thus favor survival whether the animal is predator or prey. Reduced visibility is the essential factor for survival, and appropriate color and patterns are means to obtain it. It is in this context that Gloger's generalization on albedos may be applicable to man.

Clearly the greater the amount of visible light absorbed by an animal's surface the less it will reflect, and this effect remains proportional to the amount of incident light. As reported by Martin (1930) a fine white skin will reflect 45 per cent of the incident light, a brunette 35 per cent, and the Negro a mere 16 per cent. These are therefore the respective amounts of light that under any identical condition will be available to the retina of prey or predator. As the amount of incident light diminishes, first the Negro, then the brunette and last the white will approach invisibility and the reverse of this order will attend increasing amounts of illumination.

When available light intensities decrease, the diameter of an animal's iris expands, but it will do so only in response to the amount of incoming light and the total albedo of the general scene, and it will not accommodate in order to permit examination of a small dark object, nor see into the shadows beyond an illuminated screening foreground. In effect, the brightly lighted general scene conceals from view all darker parts of the area, whereas the eye can detect and examine an object of approximately equal reflectance. This phenomenon of vision is frequently experienced but seldom consciously recognized; we encounter it when looking toward a wooded

area and failing to detect darker objects within the shadows, or while using a flashlight at night in order to see some object immediately behind a foreground of light-reflecting foliage.

Within a dark area in a forest or under reduced illumination of dawn, dusk, or a heavily clouded sky, dark objects are inconspicuous whereas light-reflecting objects become conspicuous, and their visibility is precisely correlated with the amount of light and wavelengths they reflect. In a similar manner, whether predator or prey, when an animal that is seeking to escape detection crouches in cover at the edge of forest, trail, or in a patch of shade, it will be inconspicuous to a degree that predominantly depends on matching the over-all and especially the foreground albedo.

For precisely these reasons a black-skinned man living in forests, jungle, the African "bush," or grass more than five feet in height should always be far less conspicuous, that is, far more successful than one with a white skin. Only in areas having a high degree of illumination and reflectivity would a blond or light brunette be less conspicuous.

The most incontrovertible evidence for the concealing values of dark skins in tropical forested areas came from our combat troops in the Pacific campaigns (and night-fighting commandos elsewhere) when in all but the last instant of hand-to-hand combat survival depended on seeing the enemy first and not being seen. Under these conditions even the moderately dark-skinned Japanese found it desirable to reduce their albedo by additional darkening of exposed surfaces of their bodies. Of all the troops engaged in combat in the tropics, only the Negro, Fijian, and Melanesian fighters came with adequate built-in concealment.

It seems probable that in at least one, strongly illuminated geographic area the principle of matching albedo has been reported in man. As stated by Baker (1958), but in context with adaptations to high temperatures and not concealment:

> The skin colors of desert populations have not been accurately measured, and we must rely on subjective judgments for estimates of melanin content. On this basis the desert groups appear to conform quite well to the model criteria of brunette skin. The darkest desert people are probably the Negroes who inhabit the southern fringes of the Sahara or perhaps some of the Australian groups; the lightest people are some of the North African Berber groups. Between these extremes are such groups as the Bushmen of the Kalahari, the Papago of the South Western United States desert, the other Mediterraneans of the Sahara and Near East areas. Thus as a generalization, we may say that hot desert populations are intermediate in skin melanin content.

It is possible that the Berbers may represent some gene admixture from the north, but this would not be true of the Bushmen and light-skinned Hottentots, probably two of the oldest and purest indigenous groups of the African continent. Because of their very simple cultural attainments the last two groups are closely integrated with their environment, that is, have fewer technological defenses, clothing and shelter, than the North African Berbers and Arabs, and their albedos closely conform to their desert environment.

In an earlier paragraph it was stated that the human occupants of tropical environments should have emulated some of the other animals and possessed not only a dark background color but should have been dappled or striped. From this, it is logical to suggest that whatever conscious motives underlay the widespread custom of putting on war paint prior to battle, the results may have contributed to survival by such an appreciable margin as to confirm and perpetuate its use. There can be little doubt that many of the paint daubs would have accentuated the value of a dark skin. Of course, no other animal has such an ability to put on, vary, test and wash off its pattern, and man could have improved on this already jungle-adapted albedo and adjusted it to many other environments by the simple expedient of altering the amount and distribution of his war pigments.

THE AVERAGING FACTOR IN CONCEALMENT

A common criticism of the "theory" of concealing coloration is that it is only partially effective and usually under only special conditions. The same could be said of human skin color. The reasons for seeming exceptions need not be reviewed here, but it is pertinent to point out that exclusive of the more or less continually wet equatorial tropics there is an alternation of seasons, dry alternating with wet, cold with warm, freezing with hot, brown vegetation with snow and vernal green and mature summer green, as well as many intervening permutations of these, all producing major changes in an organism's specific niche. These changes completely interdict the development of a perfect, specific, and universal livery except in extremely localized and sedentary animals having such brief life spans that they transgress neither the boundaries of their micro-domains nor seasonal changes. For all other animals except (in a somewhat lesser degree) those with changeable color or seasonal change in plumage or pelage, compromise patterns must provide against the wide latitude of environment or change that the animals may experience.

For naked creatures that do not moult, variegated patterns have partially solved the problem for some; changeable color, as in the chameleons, has also served reasonably well (even though the changes are not mediated by color vision but by light, heat and emotional reactions); but in almost all instances of concealment whether by pattern, seasonal moult, ephemeral, or transient seasonal color change, the resultant matchings are a statistical compromise.

VISIBILITY AND MORTALITY

There are numerous associated factors that may have enhanced the value of concealment for evolving hominoids and hominids, and although they are to be found in an apparently unrelated area of man's biology, a brief allusion to them may assist in understanding the total role of concealing coloration.

Evolving man was doubtless weaponless and fireless and, in the tropics at least, naked, for an immensely long time and this should have been the definitive period for establishing his basic biological traits. Through this phase of development such simple weapons as he had would have required him to accomplish the almost impossible feat of approaching his game to within arm's length or at least to within effective stone or club throw. Under these conditions the degree of his visibility would have determined the success of his food-getting. If these hunters had lived in heavily forested or "bush" areas, or jungle, or even if they had done most of their hunting in the cool of the day, at dawn or dusk, a low albedo hence a dark or black skin would have been critically important for success. As an example, it is inconceivable that a naked white-skinned tribe could have maintained itself if severe shortages of other foods forced them to adopt the elephant-killing tactics that are still, or only very recently were, successfully employed by some black-skinned African hunters. These men creep up to elephants and hamstring them with hand-held weapons. The mortality rate in white-skinned hunters using these tactics probably would equal or exceed the family or clan's birth rate.

If stones and clubs antedated fire, man must have existed on essentially equal terms with the local predators with whom (even now) he often must have contended for possession of "kills." In these encounters or even while killing large but less formidable game, minor accidents that impaired a hunter's effectiveness even for a few days or weeks could have jeopardized the entire family.

Man's effectiveness in killing large animals should have resulted in freeing him from the need to contend with larger predators for the often decomposing remains of their kills. This advance alone would have reduced danger from the other carnivora as well as presumably decreasing the frequency of illness from food poisoning. Additional benefits accruing from his ability to kill large animals for himself would be a decreasing incidence of exposure to the many diseases that can be contracted by handling or eating many small creatures. Among these diseases are anthrax, plague, tularemia and some other severe bacterial contagions, as well as the somewhat less deadly metazoan parasites. Each kill of a large animal should have provided an amount of food equivalent to an equal weight of small animals, rodents, sciurids, or lagomorphs, and if irrespective of size the incidence of communicable diseases was even approximately the same, the availability and use of the large animals would drastically reduce the probability of contact with diseased animals. Because of their complete ignorance of contagious diseases, hygiene, sanitation, or the desirability of cleanliness (the possibility of this being effective without soap is questionable), incomplete cooking, and the eating of weak or moribund prey, exposes primitive hunters to the full effects of uncontrolled chance contraction of diseases. Survival must have been achieved only on innate capacity to resist infections or recover from them, and on a high birth rate.

The roles of concealing color are multiple in animals with food habits such as those of primitive man, for it not only promotes effectiveness in food-getting with the numerous incidental gains such as those mentioned above, but also reduces the susceptibility of the animals to discovery and surprise attack by the surrounding visually cued predators, principally the felids. Leopards are crepuscular and nocturnal, or may hunt during the daytime in rainy or cloudy weather. Lions may engage in hunting at any time, but the man-eaters like leopards seem to prefer conditions of greatly reduced illumination.

Although the rarity of man-eating big cats today makes them a minor factor in human natural selection, it is doubtful if this would have been the case until long after man had developed weapons and techniques that ultimately made him an object of fear. Other primates are a favorite food of the nocturnal leopards and man must have been merely another primate to predators until he became dangerous. Furthermore, feeding patterns are at least partially implanted in the young predators by their parents, and man's capacity and determination to kill offending members of these large animals and his vengefulness toward man-eaters must have resulted in gaining for him the relative but still not complete impunity that is observable in Africa and some parts of India and Malaya today.

Judging by the wandering behavior of primates such as the family groups of semi-terrestrial baboons, monkeys and of African man, during their frequent food forays, and wood-gathering excursions in man, there is sufficient similarity in behavior among the young to warrant the speculation that the uncontrollable straying propensity of temporarily unguarded children and the frequent isolation of small laggards would have made them the most common victims of predators. (Actually, one need only observe our own children and automobile traffic in order to understand this hazard.) Here again, reduced visibility would have contributed to survival of those possessing it, whereas the conspicuous individuals would have been most vulnerable. In Natal and Zululand even as late as 1900 stilt-supported watch towers were constructed at the garden edges for the use of the children who guarded the grain and vegetables from birds, monkeys and antelope, the Zulus' explanation being that the custom was a relic of the days when predators might have attacked the otherwise defenseless young.

PREDATORY MAN AS A FACTOR

The role of man himself in the natural selection of an appropriate hue for concealment must for a long time have been an important factor contributing to the ultimate acquisition of his albedo. Man is visually cued and hence he is largely dependent on what he can see. His sense of smell is limited as compared with many other organisms, and in any event this sense is useful in only one direction, down-wind from an enemy. Hearing is less effective than vision in warning of danger or its precise direction, therefore man's safety lies primarily in his vision.

Head hunting, rape, capture of women and children for concubinage or slavery, and war for the sake of male prestige or even for sport, even today are common characteristics of some human societies, and have not been effectively suppressed even under the intolerant rule of colonial powers.

Where family, clan, or tribal desires have not been suppressed by a superior power, raiding for food, cattle and other livestock is usually a recurrent activity. Man's special proclivity for making the coincidental or premeditated capture of women his greatest reward in war, attended by the usual necessity of killing their prior owners, should have produced the conditions for selecting and multiplying the victor's genic endowment.

PIGMENTATION OTHER THAN NEGROID

The question of pigmentation in man other than the Negro requires somewhat more speculative probing, because our present knowledge of the origin and dispersal of the species *Homo sapiens* or its predecessors is not sufficiently known.

I am reluctant to undertake the necessary guessing, but those on whom the primary ideas have been tested virtually insist on an additional explanation for "brown," "yellow," "red," and "white," pigmentation. Because all of these subspecies must have reached their present areas after diffusion or migration from some center of dispersal, and presumably been susceptible to pressures of the kind that would be involved in processes of radiative adaptation common in other organisms, it is difficult to explain such misfits as the dark Eskimos and the "white" Europeans solely on the basis of their *present* distribution.

I must leave to ecologically inclined anthropologists with paleoclimatic-phytopaleontological training an explanation for "red" versus "yellow," or these versus "brown" or "white." I believe that clothing, weapons and defensive tactics may have antedated the origin of the white-skinned people and thus reduced the survival value of appropriate albedo to a subordinate status.

NEGRO POPULATIONS OUTSIDE THE TROPICS

If man originated within the tropics and was thus adapted to these conditions, the present distribution of the Negro far beyond the limits of tropical forests presents a seeming contradiction to the concealing value that I have ascribed to his albedo. If he had been so well adapted to the special environment of dense forests, he must have been equally conspicuous in highly illuminated areas. Concealing coloration cannot have worked both ways. The more perfect a given concealment is in one ecological setting, the more conspicuous it becomes in a contrasting one, hence if concealment had been so significant in the one setting as I have proposed, then some wholly new development, or developments, ultimately must have enabled the possessors of a negroid albedo not only to dispense with this trait, at least to a great extent, but to thrive despite its handicap.

It seems reasonable to suppose that with the accumulation of developing social, technical and cultural advances, especially in the area of progressively more effective weapons, probably increasingly supplemented by the use of fire, he ultimately acquired the characteristically human type of evolution that permitted him to survive almost anywhere. It is precisely and chiefly, if not only, by technological and social developments that man has increased the gap between other mammals and himself and become increasingly emancipated from natural selection.

Even such a seemingly minor acquisition as the olfactorily guided domesticated hunting dog would have neutralized to a significant degree the value of visual abilities and its sequel, effective concealment, in any region and from any type of enemy. Because of their superior olfactory sense reinforced by their independent scouting and loud barking, dogs at once added important new dimensions to man's own biological capacities. Because most dogs range widely and are chiefly dependent on their sense of smell, and because they announce their discoveries vocally, they virtually extend man's perception to much greater distances. Their role in cancelling the advantage of visual concealment and exposing hidden danger, as well as in discovering game and revealing it to their master, must have had survival value far greater than has been credited to them.

CONCLUSION

From the foregoing speculations it seems reasonable to presume that pigmentation, like numerous other morphological traits of man, has persisted long after its utility had been reduced by changes in his way of life. If this proves to be the case, we can look upon this vestigial remainder of a very remote past as an inconsequential relic except for the uses to which human differences have been used to support unhumanitarian prejudices.

SUMMARY

The putative physiological values of skin melanization of many tropical peoples do not withstand critical examination. If these supposed physiological benefits cannot be supported, then it is desirable to investigate the possibility that the distribution of low albedo skin color may be explained on some other basis.

Because we perceive objects only in terms of visible wavelengths of light, and because the visible range includes some 50 per cent of the incoming radiation, interpretation of the role of differing albedo is more logically limited to functions associated with light that can be seen than to the invisible infrared and ultraviolet that cannot.

On this basis it is proposed that the concealment factor innate in differing albedos in areas of differing light intensities and environmental illumination proffers a reasonable hypothesis by which to explain some of the variations in human melanization, especially as observed in "black"-skinned people.

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STUDIES OF THE RELATIVE FITNESSES OF EXPERIMENTAL POPULATIONS OF *DROSOPHILA MELANOGASTER**

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INTRODUCTION

The concept of the fitness of a population is extremely elusive. Individual members of a Mendelian population differ as to the number of offspring they produce; consequently, their contributions to the composition of succeeding generations differ. One can speak, then, of these individuals differing in relative fitness. Furthermore, if some aspect of the genotypes of these individuals is responsible for their net reproductive potentials and if these genotypic differences can be identified conveniently, the estimates of relative fitness can be referred to the responsible genotypes rather than to the individuals themselves. Studies on the fitnesses, or adaptive values, of different genotypes have been made for a number of species (Moser, 1958, bacteria; Dobzhansky, 1951, 1955, Drosophila; Allison, 1955, man). In many instances it is impractical or impossible to define the genetic constitution of individuals and, consequently, adaptive values cannot be ascribed to specific genotypes. Confronted with this situation, the investigator can study either the range of fitnesses of different individuals or, if suitable techniques are available, the range of fitnesses exhibited by individuals possessing a variety of gene combinations typical of those found in the population. More precisely, the investigator can study some of the components of fitness such as longevity, survival under competition, fecundity, or a combination of these components under a set of specified environmental conditions; he must then assume that this information applies generally to fitness itself under these same conditions. In this laboratory we have used the genetic techniques available for Drosophila to estimate distributions of fitness in individuals carrying random combinations of second chromosomes obtained from certain experimental populations of *Drosophila melanogaster* (Wallace, 1951, 1956; Wallace and King, 1951, 1952).

Information regarding the array of adaptive values of individuals or, better, of certain genotypes within populations may, under certain circum-

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The editorial policy of THE AMERICAN NATURALIST ordinarily does not permit such detailed publication of statistical information as that seen in the present paper. The Editorial Board, however, felt in this case that the data were essential to the argument and the author has supported the cost of the tabular publication through his research contract.

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stances, lead to predictions regarding future phenotypic or genotypic constitutions of these populations. Making such predictions is essentially the task confronting the animal or plant breeder who regulates artificially the reproductive abilities of different individuals. Similarly, the student of the genetics of human or other populations who undertakes to predict the genotypic arrays to be found in a population left to its own devices for a number of generations (see, for example, Glass and Li, 1953) relies, in making these predictions, on a knowledge of the adaptive values of different genotypes.

The fitness of a population is not the same as the average relative fitness of its individual members. The numerical value describing these relative fitnesses is based upon an arbitrary choice of an internal standard of measurement: if a high choice is made, the population average will appear low; if a low choice, the average will appear high. It would seem, though, that when the average relative fitness, whatever its basis, is maximized through alterations in genotypic proportions, so is the fitness of that population (Li, 1955).

If the fitnesses of the individual members of a population (or of individual genotypes characteristic of these individuals) are determined not with reference to one another but with reference to an external standard under a given set of experimental conditions, one can justifiably claim that the momentary fitness of the population relative to that standard and under the conditions of the test does in fact equal the average of these individual fitnesses. At best, however, this estimate of fitness is only an approximate one. First, the population itself usually does not exist under the environmental conditions characteristic of the individual tests. Second, the individuals (or individual genotypes) are tested one by one while the population fitness encompasses interactions between individuals as well (Levene et al., 1954).

A measure of the momentary fitness of a population, although better than no measurement at all, is of but limited interest. The measure one really wants to make when describing a population is that which refers to its ability to perpetuate itself through time under a certain set or sequence of environmental conditions. It is not satisfying, for example, to observe (as we do periodically in the case of tent caterpillars) that a population doubles or trebles in size in a given generation and to conclude from that observation that the population possesses a high fitness. It would be more informative to observe a population for a number of generations in a variable environment and attempt to estimate the probability that, faced with an array of environmental conditions of which the several observed ones represent a random sample, the population will continue to exist for a specified number of future generations. (The probability that any population will continue for an infinite time is zero; this, however, is not a particularly profitable value to adopt for general use.) Fitness as estimated in these ways is related to the concepts of adaptedness and adaptability (see Thoday, 1953, and Lewontin, 1957).

We are confronted with purely hypothetical situations when attempting to discuss the relative fitnesses of two or more populations of the same species. By definition, two such populations cannot be sympatric; co-existence would merely lead to their fusion into a single new population. On the other hand, to deny the existence of relative fitnesses of populations of the same species is scarcely reasonable. One would not claim, for example, that a mutant strain of flies carefully tended in the laboratory is equal in fitness to a natural population of the same species simply because the diligence of the stock-keeper guards the mutant stock against extinction. One would prefer, rather, to compare the respective probabilities that either population would become extinct if the two faced identical environments or identical series of environmental changes.

In the case of human populations this problem is very real. We are faced with the necessity of choosing one of several possible courses of action regarding the use of mutagenic radiations; it is necessary to estimate the probable effects of these different courses of action on human populations and, then, on the basis of these theoretical considerations to adopt that course which seems least harmful.

How does one estimate the relative fitnesses of two populations of the same species? As an exercise in imagination, one can visualize two populations separated by an infinitely flexible, elastic membrane, a barrier that would permit all aspects of co-existence except interpopulation matings. One could then observe these two competing populations generation after generation until one became extinct; the relative fitnesses of the two could then be expressed as a probability function of extinction. One could also confine his observations to a limited number of generations and make predictions based on these observations. These are essentially the procedures used by Park in his studies of the competitive abilities of two *different* species of the flour beetle, Tribolium (Park, 1948). In practice, one can only attempt to manipulate available techniques in an effort to get information that lends itself to the same sorts of calculations.

In previous studies (*op. cit.*) we have used a measure of fitness analogous to, but not identical with, Wright's $\overline{W}$ to estimate the relative fitnesses of experimental populations of *D. melanogaster*. These studies have been limited to the second chromosome, that is, to about two-fifths of the entire genome of the species. The components of fitness studied have included egg, larval, and pupal survival and developmental rates in half-pint culture bottles. Our estimates of individual $\overline{W}$'s (estimates relating to genotypes, not to individuals) were made relative to flies of a standard genotype which were not part of the population under study. The comparisons of populations were made by equating the standards, by adjusting the estimated $\overline{W}$ of one population to 1.000, and then by recomputing the $\overline{W}$'s of all other populations. These estimated $\overline{W}$'s are not intended to be estimates of absolute fitnesses; they are, however, taken as indications of relative fitnesses.

The experiments described below attempt to eliminate some of the more obvious shortcomings of the genetic techniques previously used. In the

present experiments estimations of adaptive values are based on the number of adult offspring produced by single pairs of individuals drawn at random from different populations. The apparent advantages of this technique over the genetic test described above are as follows. First, many components of fitness are subsumed by this test—mating ability (including actual sterility); fecundity of females; egg, larvae, and pupal mortalities under crowded conditions; and speed of development. Second, the entire genome rather than the second chromosome alone is tested under these conditions. Third, there is no need to cross the tested flies with unrelated, genetically marked strains and, hence, the formation of novel gene combinations is avoided. The simultaneous inclusion of more components of fitness and of more of the genome of the tested flies can be expected to lead to larger differences between the estimated fitnesses of different populations than those revealed by the earlier genetic tests (see also Knight and Robertson, 1957). The problem of novel gene combinations is not eliminated by this technique; it will become apparent that these arise within the experimental material even in the absence of outcrossing.

MATERIALS AND METHOD

The experimental populations of *D. melanogaster* to be compared in the present experiments are designated by the numbers 1, 3, 5, 6, 7, 17, 18, and 19. Pertinent information regarding the ages, sizes, and radiation histories of these populations is listed in table 1 (see Wallace, 1956, for additional information). The results of earlier genetic analyses of these populations are to be found in the publications of Wallace, and Wallace and King, mentioned above.

TABLE 1

Details of the experimental populations

Pop.	Origin	Size	Exposure	Dose	Date started
1	Stocks	Large	Acute, x-rays	7000r ♂♂ 1000r ♀♀	July 25, 1949
3	Stocks	Large	None	...	July 25, 1949
5	Stocks	Small	Chronic, gamma-rays	5.1r/hr	April 1, 1950
6	Stocks	Large	Chronic, gamma-rays	5.1r/hr	April 15, 1950
7	Stocks	Large	Chronic, gamma-rays	0.9r/hr	April 15, 1950
17	5-125	Small	None	...	April 27, 1954
18	5-125	Large	None	...	April 27, 1954
19	6-126	Large	None	...	May 15, 1954

Each individual experiment of the present series consisted of determining for ten (occasionally for only eight) consecutive generations the mean number of offspring produced in 1" × 4" shell vials by 50 single pairs of flies drawn initially from each of two populations. With the exception of the original pairs of flies, the parents for each generation were obtained from the fertile vials of the preceding generation. No radiation was administered to the flies during these experiments.

The flies used in the first generation of each experiment came from egg samples taken from the appropriate populations; the samples were placed in half-pint culture bottles containing medium enriched with brewer's yeast. Fifty males and 50 virgin females from each of two "competing" populations were mated as single pairs in shell vials which were kept at 25°. The flies hatching in these vials were counted first on the ninth day and again on the fourteenth day. At the time of the first count, the numbers of sterile matings were scored. During this count, too, males and virgin females were obtained which were used to set up 50 new vials for each of the two populations on the fourteenth day, the day of the last count of the previous vials. With rare exceptions when three or four flies of one sex only were obtained from a vial, two males and two virgin females were chosen from each vial to be parents for the next generation. Sexes were stored separately for the five-day interval from the ninth to the fourteenth day; males and females collected from different vials, however, were stored together. Consequently, the parental crosses for each new set of 50 vials consisted of random matings of males and females obtained from the different fertile vials of the preceding generation. In effect, the 50 vials representing a single experimental population comprise a small splinter of that population, the effective population size of which was somewhat less than 100 flies, and which was usually perpetuated for ten generations.

The vials used in these experiments contained regular agar-cornmeal-molasses medium enriched with brewer's yeast. The amount of medium in each vial was not measured but, within any one generation, it was relatively constant from vial to vial. Furthermore, the vials to be used for two competing populations were chosen haphazardly from the same tray of freshly prepared vials so that those with different amounts of food would be distributed equitably between the two populations.

A number of persons arranged the mating and counting of flies for these experiments. To reduce uncontrolled variations to a minimum, each experiment involving the competition of two populations was handled by one person. If at any time help was needed by the person responsible for a set of "competing" flies, the task involved was divided in such a way that both populations were handled by the two persons to an equal extent. During the course of the experiments (roughly nine months) the original food-maker resigned; the number of flies hatching per vial decreased with this change in personnel. Since the analyses of the experimental data involve comparisons of two "competing" populations in each generation, this change does not seriously affect the outcome of the experiment.

EXPERIMENTAL RESULTS

The studies described here consist of 28 experiments in each of which two populations have been allowed to "compete"; all combinations of our eight populations, taken two at a time, have been included among these tests.

TABLE 2

Starting dates of experiments involving different pairs of "competing" populations

Populations	Start	Populations	Start
1 vs 3	1/3/56	5 vs 7	8/13/56
1 vs 5	6/20/56	5 vs 17	6/26/56
1 vs 6	6/19/56	5 vs 18	6/4/56
1 vs 7	1/16/56	5 vs 19	7/10/56
1 vs 17	5/28/56	6 vs 7	1/18/56
1 vs 18	3/19/56*	6 vs 17	7/9/56
1 vs 19	1/16/56	6 vs 18	7/16/56
3 vs 5	1/24/56	6 vs 19	6/11/56
3 vs 6	6/5/56	7 vs 17	7/10/56
3 vs 7	7/9/56	7 vs 18	8/14/56
3 vs 17	6/4/56	7 vs 19	7/17/56
3 vs 18	1/9/56	17 vs 18	3/21/56*
3 vs 19	3/21/56*	17 vs 19	3/27/56*
5 vs 6	1/17/56	18 vs 19	1/24/56

*Experiment lasted eight generations rather than ten.

The starting dates of these experiments are listed in table 2. Unless indicated otherwise, each of these experiments extended over ten generations (20 weeks); the exceptional cases in which the populations competed for only eight generations are 1 vs 18, 3 vs 19, 17 vs 18, and 17 vs 19.

Sterility. The mean frequencies of sterile matings observed in the successive generations of vials representing the different populations in all experiments are listed in table 3. Several different patterns are apparent in these data. Populations 1 and 3 are characterized by frequencies of sterile matings which are initially low but which increase rapidly during the first five or six generations; these frequencies tend to remain at high levels for

TABLE 3

Per cent sterile cultures among single pair matings of flies of different populations in successive generations of present experiments. Unless otherwise indicated, the number of matings tested for one population in a single generation was 350.

Generation	Population							
	1	3	5	6	7	17	18	19
1	9.7	6.0	17.7	17.4	11.4	14.3	7.1	4.9
2	10.6	10.0	18.6	13.4	5.7	6.9	6.0	9.7
3	24.9	14.9	6.0	14.3	9.4	5.1	4.3	4.0
4	24.9	20.3	9.1	10.6	4.3	8.6	2.6	3.7
5	24.0	22.9	7.1	8.9	4.0	5.1	3.4	4.3
6	19.1	17.4	10.0	6.9	5.7	6.3	6.6	8.0
7	20.9	16.0	8.0	8.3	4.0	5.7	4.9	4.0
8	25.4	14.3	6.0	9.4	3.7	6.9	8.9	6.0
9	20.3*	13.7*	6.6	9.1	4.0	4.4†	6.0†	4.8†
10	12.7*	14.0*	7.7	7.1	3.4	8.0†	8.0†	3.2†

*300 vials tested.
†250 vials tested.

the remainder of the experiment. Populations 5, 6 and 7, three populations which received continuous gamma-irradiation until the moment the flies were withdrawn for these experiments, had initially high frequencies of sterile cultures but these declined during the course of the ten generations in vials. Populations 17, 18 and 19 (with the exception of the first generation of population 17) tend to have uniform and relatively low frequencies of sterile matings.

These data alone are sufficient to indicate that genetic changes of a variety of types accompany the changes in population size, mating patterns, culturing techniques, and, in the case of populations 5, 6 and 7, cessation of radiation demanded by the experimental procedures of this study. The increase in sterility among flies taken from populations 1 and 3 cannot easily be ascribed to inbreeding and chance homozygosis; the flies in these vials were, after all, members of sizable populations. There must exist in the case of these flies a selective superiority of individuals heterozygous for sterility factors; a superiority exceeding that possessed by similar individuals in the original populations. Possible sources for this added advantage in the vials lie (1) in the early collection of parents with the emphasis this places on rapid development and (2) in the mating of single pairs of flies, a mating pattern which eliminates sexual competition as a selective agent. In the vials of flies from populations 5, 6 and 7 the frequencies of sterile matings progressively decreased; sterility factors in these populations appear to be present not as the result of selection but as the result of the continuous radiation to which these populations were exposed. After cessation of radiation, these sterility factors were simply eliminated from the populations in vials. In agreement with this interpretation, relatively few of the pair matings of flies obtained from populations 17, 18 and 19 were sterile and, again with the possible exception of the first generation of flies from population 17, the frequency of sterile matings remained constant during the course of successive generations. These populations, daughter populations of 5 and 6, had not been exposed to radiation for 40 generations or more before the present series of experiments were started; elimination of sterility factors had already occurred in these populations.

If one were to use the mean proportion of fertile matings in all ten generations as a basis for estimating the relative adaptive values, one would conclude that our control population 3 and population 1, a population subjected to a single x-ray exposure some 170 generations before the present experiments, have lower fitnesses than any of the other populations. This conclusion would fail to take into account the novel gene combinations which have arisen within the "vial" populations either by accident or in response to the altered techniques for perpetuating these small populations. A more realistic procedure for utilizing the data on sterility in reference to the experimental populations would consist of restricting ourselves to data obtained in the first generation only; the first generation reflects more accurately the situations which prevail in the original populations themselves.

Nevertheless, the different patterns of change in frequencies of sterile matings among the small "vial" populations suggest still another measure of fitness for these populations: namely, the fitness of an experimental population in regard to the conditions of the present experiments.

Numbers of offspring. Initially, it was planned that the average number of adult offspring produced per single pair mating would be taken as an indication of the relative fitness of a population. The profound changes which occurred in the proportions of sterile matings of flies from populations 1 and 3 raised serious questions as to the meaning of this figure. It is quite clear that the frequency of sterile matings has changed during the course of these experiments; in some populations there has been a gradual elimination of the responsible factors while in others these factors have actually accumulated, seemingly under the influence of natural selection.

The frequency of sterile matings has a large effect on the average number of offspring when these are calculated on the basis of *all* matings. If the sterility observed in the case of populations 1 and 3 has actually resulted from a selection in favor of sterility factors, a more stable measure of the number of offspring would be the average number per *fertile* vial. The analyses which follow, then, deal exclusively with this average number.

A summary of the data on mean numbers of flies produced per fertile mating is given in table 4. The smallest number of vials upon which any of these means is based is 22; in the vast majority of instances there were more than 40 fertile vials among the 50 representing one generation of a single population. The data in table 4 reveal the large differences between the *mean* numbers of flies per vial obtained at different times and for different populations; these range from 150 or more to less than 70. In part this variation occurred while the obvious experimental conditions—personnel, temperature, and media—remained constant. However, a spectacular change in mean number occurred when our original media maker left the laboratory. For some time after this change, not nearly so many flies were obtained per vial. Gradually the number increased either because the new food maker gained experience or because of selection among the flies themselves.

The distribution of experiments involving different populations was not symmetrical in relation to the change in media; consequently the analysis of the relative yields for different populations must be based on comparisons of paired, competing populations for each generation. This fact is emphasized in table 5 where the first line gives the relative numbers of offspring per fertile mating (population 3 equals 1.00) for the first generation, computed directly from the data listed in table 4. Following this entry are eight estimates of the same relative yields obtained by comparing pairs of populations in a way described below. The last entry is the average of the eight previous ones. Obviously, populations 1 and 3 were studied largely at times preceding the change in media preparation while populations 5, 6, 7 and 17 were more often tested later. This is reflected in the improvement

TABLE 4

Mean number of offspring produced by fertile single pairs of flies from different experimental populations. The populations are tabulated as competing pairs. "Generation" refers to successive generations in vials.

Generation	1	3	1	5	1	6	1	7
1	115.88	118.10	95.96	74.75	98.81	81.95	105.98	112.34
2	114.59	111.18	88.49	74.13	81.74	84.86	101.63	127.54
3	110.47	116.10	103.63	82.24	92.88	80.30	108.90	123.52
4	108.17	111.85	89.29	72.51	91.72	94.94	120.54	134.75
5	110.56	134.88	116.76	98.90	124.02	95.56	127.60	103.92
6	118.11	126.27	127.44	99.19	109.00	96.22	127.18	117.17
7	124.73	130.56	93.95	77.98	109.64	90.65	112.50	119.22
8	110.73	138.00	94.45	81.68	79.34	67.39	106.43	127.02
9	108.13	131.70	101.50	95.87	93.06	84.12	99.00	96.21
10	76.15	105.00	85.32	90.58	84.38	61.02	98.89	102.21
	1	17	1	18	1	19	3	5
1	92.98	107.13	157.05	115.35	109.94	99.06	114.40	90.71
2	106.07	93.22	127.57	121.65	105.04	95.38	107.46	91.21
3	111.89	105.98	112.44	98.86	129.05	105.12	128.06	97.35
4	100.24	90.32	128.20	117.26	146.34	109.59	128.00	110.81
5	110.50	97.31	88.00	81.94	128.71	112.00	116.34	93.47
6	89.70	95.45	105.35	99.51	143.95	121.68	125.26	113.00
7	133.78	124.94	113.03	103.14	121.48	118.80	120.68	84.21
8	146.47	133.83	99.69	89.33	120.94	103.34	121.22	94.06
9	119.96	116.00	...	...	95.93	93.57	87.07	75.50
10	93.06	87.02	...	...	114.84	96.02	87.53	64.57
	3	6	3	7	3	17	3	18
1	101.31	86.00	88.46	101.70	107.91	102.09	120.73	116.54
2	100.44	88.57	90.08	98.65	122.75	102.89	116.15	106.44
3	110.90	87.40	113.82	132.51	115.76	103.33	123.07	106.98
4	104.95	81.79	117.68	125.27	110.31	95.06	126.31	126.22
5	108.32	88.33	128.03	137.57	103.02	92.68	127.26	122.54
6	117.78	95.40	129.76	126.74	105.63	99.08	117.25	106.06
7	121.98	97.84	96.95	98.13	132.53	121.43	128.70	114.14
8	113.00	93.47	113.84	123.47	128.61	111.96	116.79	125.91
9	81.98	68.19	115.05	104.30	75.72	82.86	120.69	126.73
10	111.59	85.80	108.23	102.92	119.85	102.15	84.23	84.39
	3	19	5	6	5	7	5	17
1	139.65	118.00	92.57	90.78	88.40	114.15	75.23	88.46
2	142.21	128.69	104.84	101.16	104.76	129.52	92.57	107.04
3	113.70	115.94	105.16	99.95	98.81	119.92	98.25	108.65
4	98.63	84.57	114.89	117.36	62.82	86.06	81.65	94.82
5	100.63	82.96	115.98	117.77	101.32	111.07	114.71	120.06
6	113.77	95.75	116.96	116.76	79.40	103.55	108.94	129.00
7	120.12	110.19	125.09	125.30	81.15	103.65	77.64	92.18
8	94.90	76.74	111.28	101.34	76.02	91.69	87.50	94.45
9	...	...	88.80	88.78	76.74	94.20	90.23	106.10
10	...	...	91.79	81.13	73.56	88.90	83.16	88.44

TABLE 4 (*continued*)

Generation	5	18	5	19	6	7	6	17
1	87.74	100.04	83.73	72.17	88.71	116.87	67.08	83.86
2	71.37	100.98	82.41	79.67	92.00	120.06	68.42	87.68
3	87.02	98.41	84.02	80.07	96.28	112.57	73.03	95.77
4	96.10	95.51	101.47	97.34	88.53	135.96	90.52	130.18
5	81.75	99.27	108.64	112.78	99.71	136.58	113.07	122.12
6	98.43	92.58	82.09	86.55	129.16	150.56	96.87	109.69
7	117.26	119.02	86.04	87.89	99.96	139.78	75.32	83.31
8	102.98	123.30	94.60	109.04	106.65	132.98	84.84	110.60
9	74.84	76.98	84.83	93.72	66.90	96.53	78.77	94.98
10	95.00	104.50	74.53	82.64	75.85	96.09	69.94	97.04
	6	18	6	19	7	17	7	18
1	73.90	81.78	96.31	103.04	94.17	80.30	130.17	108.51
2	78.61	88.62	97.64	99.94	98.25	102.33	130.92	113.41
3	86.21	103.62	78.43	84.04	101.05	98.77	120.57	110.65
4	87.48	121.94	84.02	87.29	128.41	113.86	85.35	81.20
5	90.73	113.04	72.83	78.80	134.18	120.77	111.00	110.71
6	64.68	77.60	98.73	113.92	97.31	90.54	90.69	89.24
7	83.49	109.70	96.77	119.98	86.75	99.45	109.80	106.81
8	71.37	92.17	77.47	107.53	99.11	108.04	85.00	85.46
9	75.17	85.96	68.89	76.67	101.34	104.58	82.49	78.92
10	68.76	88.29	76.35	91.76	87.77	81.96	101.15	96.31
	7	19	17	18	17	19	18	19
1	75.43	73.98	121.88	121.65	122.33	135.24	100.04	95.27
2	110.96	88.11	119.40	113.72	121.88	109.55	103.60	98.55
3	124.12	100.00	135.43	127.78	119.22	111.60	114.67	104.10
4	123.90	105.48	128.43	123.42	100.54	94.68	113.74	107.94
5	113.17	96.50	94.49	89.91	87.98	94.48	112.17	111.02
6	90.55	76.42	96.56	89.46	100.76	93.54	123.22	113.23
7	112.92	95.25	127.36	103.49	96.13	103.66	137.00	88.47
8	89.29	71.58	93.58	69.88	91.24	90.36	136.09	98.89
9	113.43	86.89	...	...	...	...	89.73	75.06
10	88.76	74.93	...	...	...	...	112.82	96.13

shown by the latter populations when their performance is measured for each individual experiment relative to the competing population studied at that time. Even the relative standings of populations 1 and 3 are reversed by this type of calculation; not one of the eight estimates of fitness of population 1 for the first generation falls below 1.00 when calculated by the second technique.

The calculations of relative fitness based on individual pairs of competing populations are rather time-consuming. The procedure is as follows: One population is chosen as the standard and an initial estimate of the relative fitnesses of the other populations is obtained by dividing the mean numbers of flies produced by pair matings of these other populations by the mean numbers produced by the flies of the standard population in every experiment where the standard competed with one of the other populations. (Let *a*, *b*, and *c* be three populations and let *a* be the standard. The initial estimates of fitness for populations *b* and *c* are obtained from the experi-

TABLE 5

Relative numbers of offspring produced per fertile pair mating of flies from different populations in the first generation in vials. The figures in the first row are relative numbers based on uncorrected numbers obtained from table 4. The next eight rows are relative numbers obtained by comparing each pair of competing populations as explained in the text; each of the eight populations has been used in turn as a standard for these comparisons. The last row is the average of the preceding eight.

Standard Pop.	1	3	5	6	7	17	18	19
	.98	1.00	.75	.74	.94	.89	.94	.88
1	1.01	1.00	.86	.82	1.08	.94	.94	.91
3	1.02	1.00	.85	.83	1.07	.97	.90	.92
5	1.03	1.00	.85	.83	1.09	.98	.92	.94
6	1.01	1.00	.84	.81	1.07	.95	.90	.90
7	1.00	1.00	.83	.81	1.05	.95	.89	.86
17	1.04	1.00	.86	.83	1.06	.95	.90	.89
18	1.01	1.00	.83	.81	1.06	.96	.89	.90
19	1.04	1.00	.82	.83	1.11	1.00	.92	.90
Average	1.02	1.00	.84	.82	1.07	.96	.91	.90

ments *a* vs *b* and *a* vs *c* by dividing the mean number of offspring in the *b* and *c* vials by the mean number in the corresponding *a* vials.) An additional estimate of the fitness of the other populations can be obtained by utilizing these initial estimates and the results of the additional competing combinations. Hence, referring to the example, an additional estimate for population *b* can be obtained by multiplying the ratio of *b/c* from the *b* vs *c* experiment by the first estimate of fitness obtained for population *c* (this amounts to $b/c \times c/a$ or b/a, another estimate of *b* relative to *a*); the second estimate of fitness for population *c* is obtained in a similar way by multiplying the ratio *c/b* from the *b* vs *c* experiment by the initial estimate for population *b*. Because of the labor involved, a full calculation in which each of the eight populations was given an opportunity to serve as the standard was made for the first, second, fifth, eighth, and tenth generations only. In the remaining generations, population 3 was the sole standard; the magnitude of the error incurred by this restriction can be judged by comparing the individual entries of table 5 with the average of these entries. (A similar type of analysis could have been used in comparing the frequencies of sterile matings. A preliminary calculation indicated that the more laborious computation did not alter the results obtained by the simpler method. Apparently environmental conditions affect numbers of offspring to a much greater extent than they affect the success or failure of a single pair mating.)

The estimates of fitness based on the mean numbers of offspring produced by fertile, single pairs for the different populations in the ten consecutive generations of the present experiments are listed in table 6. These estimates are relative to that of population 3, which is always listed as having fitness of 1.00; there is no way by which the successive generations of population 3 can be compared in order to reveal any absolute change in fit-

TABLE 6

Relative numbers of offspring per fertile, single-pair mating of flies from different populations in ten successive generations in "competing" vials. These data have been computed by the method described in the text.

Generation	Population							
	1	3	5	6	7	17	18	19
1†	1.02	1.00	.84	.82	1.07	.96	.91	.90
2†	.97	1.00	.83	.85	1.08	.97	.96	.87
3*	1.00	1.00	.85	.81	1.03	.97	.93	.84
4*	.99	1.00	.83	.79	1.08	.96	.94	.84
5†	.99	1.00	.81	.78	.96	.87	.93	.86
6*	.99	1.00	.82	.81	.98	.96	.91	.86
7*	.95	1.00	.81	.75	.98	.95	.95	.85
8†	.93	1.00	.80	.74	.99	.96	.95	.85
9*	.95	1.00	.86	.82	1.02	.97	.94	.85
10†	.85	1.00	.79	.69	.92	.86	.90	.79

*Population 3 used as standard; compares with single entry in table 5.

†Each population used as standard in turn; values listed are average values comparable to average listed in table 5.

ness of this population during the course of the experiments. The table reveals a number of interesting facts. In the early generations, population 7 gave consistently greater numbers of offspring per mating than did the standard population (No. 3); population 7 had been exposed continuously to approximately 300r gamma-radiation per generation for about 150 generations prior to these experiments. Similarly, in the first generation within the competing vials, population 1 produced more flies than did the standard; as mentioned above, every estimate of fitness listed for this population in table 5 is 1.00 or higher. Populations 5 and 6 produced on the average somewhat better than 80 per cent as many flies per mating as did the control population; these populations had been exposed to some 2,000r gamma-radiation per generation for about 150 generations preceding these studies. Finally, populations 17, 18 and 19, daughter populations of 5 and 6 (see table 1), produced about 90 per cent as many flies per fertile pair as did the standard.

A second interesting feature of these data lies in the relative changes which occurred during successive generations in these vials. In general, each of the large populations with a history of radiation showed a decline in the relative number of offspring produced by fertile pairs of flies. There is, of course, no way of evaluating these changes in absolute terms; it is impossible to tell, for example, whether all populations improved, with No. 3 improving most rapidly, or whether all populations suffered a decline with the standard population declining most slowly. We can see, however, that relative to population 3, populations 1, 6, 7 and 19 undergo a rather systematic decline in the numbers of offspring per vial. To say that all large populations with radiation histories decline in offspring production under the conditions of these experiments means little, unfortunately, since all

large populations except population 3 had radiation histories. It would be more meaningful if there were several non-irradiated control populations which could be compared one with the other in order to estimate the relative changes undergone by non-irradiated populations. Nevertheless, the statement does become more meaningful when it is pointed out that small populations (Nos. 5 and 17) or a population derived from a small population (No. 18) show this decline to a much smaller extent than do the others. Thus, single pairs representing population 5, with the exception of the tenth generation, consistently gave about 80 per cent as many offspring as the control. Population 17, a small population obtained originally from No. 5, gave (with the exception of generations 5 and 10) about 95-97 per cent as many flies per mating as did the control. And, finally, population 18, a second daughter population of No. 5 but one which was allowed to increase in size, gave more than 90 per cent as many offspring per fertile pair as the control through all ten generations.

An explanation of the above facts which is consistent with the decline in productivity of individual pairs of flies from our large populations under the present experimental conditions, with the absence of a similar decline in the case of small populations, and with the initially high productivity of populations 1 and 7, is to be found in the role of mutations in heterozygous condition. If we assume that the effect of a mutation in heterozygous individuals is not rigidly correlated with the effect of the same mutation when homozygous (witness the selection for sterility factors in the vials containing flies from populations 1 and 3!), the presence of many mutations in a population is to be explained by selection favoring them in heterozygous condition. The efficiency of this type of selection is greater in a large population than in a small one, for in the latter the role of mutations in homozygous condition assumes greater importance. It is this exaggerated role of homozygosis in small populations that accounts for the observed decline in productivity in the case of the large, irradiated populations in the present studies; the technique for maintaining flies in vials imposes a severe restriction on population size, a restriction that is alien to the past histories of these populations. In the small vial populations, flies became homozygous for genes and for combinations of genes the existence of which depended initially upon their behavior in heterozygous condition. The fact that the average productivity for population 7 seemingly exceeds that of the control in early generations, while that of population 6 does not, suggests that fitness is not a precise function of mutation rate. This implies that not all induced mutations are unconditionally deleterious. It suggests, however, that there are rates of mutation which exceed the capability of selection, even selection for heterozygous individuals, to cope with the influx of new mutations.

The data listed in table 6 give the average relative productivity based on all of the experiments in which each population took part. It is interesting to inquire into the variation exhibited by different samples of flies from the same population and, in addition, the variation exhibited in successive

generations of the same sample. Again these questions can be approached only through the interrelations of paired populations.

Table 7 lists, as an example, the productivity of fertile pairs of flies from population 3 relative to each of the other seven populations with which this population competed. The figures listed in this table were obtained by adjusting the mean number of flies produced by the non-control, single-pair matings in each generation by the average productivity of that population in that generation listed in table 6. The ratios of the mean number of offspring in the control vials (population 3) to the adjusted figures of the competing

TABLE 7

Adjusted mean numbers of offspring per single pair mating of flies from various populations relative to the mean number of offspring produced by flies from population No. 3 in those experiments involving population No. 3. The actual mean number of flies produced in each generation by the non-control population has been adjusted by the values listed in table 6 so that, in the absence of variation between samples of flies or between generations of the same sample, each entry in this table is expected to be 1.00.

Generation	Population						
	1	5	6	7	17	18	19
1	1.04	1.06	.97	.93	1.01	.94	1.07
2	.94	.98	.96	.99	1.16	1.05	.96
3	1.05	1.12	1.03	.88	1.09	1.07	.82
4	1.02	.96	1.01	1.01	1.11	.94	.98
5	1.21	1.01	.96	.89	.97	.97	1.04
6	1.06	.91	1.00	1.00	1.02	1.01	1.02
7	.99	1.16	.94	.97	1.04	1.07	.93
8	1.16	1.03	.89	.91	1.10	.88	1.05
9	1.16	.99	.99	1.12	.89	.90	...
10	1.17	1.07	.90	.97	1.01	.90	...

vials were then calculated. If every sample of 100 flies taken from a population were identical with every other such sample, and if the changes undergone by each sample during the ten generations of these experiments were precisely the same, every entry in table 7 would be 1.00. Obviously, this uniformity is not observed. It would seem, for example, that those samples of flies taken from population 3 which competed with those of populations 1 and 17 produced exceptionally low average numbers of offspring per fertile mating or, as an alternative explanation, these particular samples from populations 1 and 17 were exceptionally good in this regard. On the other hand, in the competition between populations 3 and 6, either an unproductive group of flies was chosen from No. 6 or an exceptionally good one from No. 3.

Of even greater interest are the variations in successive generations within the same experiment involving two competing populations. It will be recalled that the data listed in table 7 have been adjusted for average systematic changes which were detected by the earlier analysis (table 6). Of the seven experiments involving population 3 which we have listed, in five

instances the range in variation amounts to 20–25 per cent of the mean value. Since these data are based on paired observations in which experimental variables were distributed equally between the two populations, these fluctuations must be either the result of fortuitous gene combinations arising in different generations of these small populations, or an indication that the individuals of different populations react specifically and in different ways to the environmental conditions prevailing in the vials of different generations. At any rate, we can conclude that the fitness of a population is not a constant. Although the mean fitness of a series of similar populations tested under a given set of experimental conditions can be described with considerable accuracy (as can any mean value), substantial fluctuations in fitness do occur.

Estimates of fitness based on combined data. In this section we will combine the information on sterility and numbers of offspring per fertile mating in an effort to obtain an estimate of the relative fitnesses of the populations from which the flies were originally taken. Because of changes which occurred in successive generations in vials, we must restrict our calculations to the first generation in attempting to assay the fitnesses of the experimental populations as they exist in their population cages. We need not, however, impose a similar restriction in attempting to ascertain the fitnesses these populations would possess were they confronted—as they were in the course of these studies—with the environmental conditions of these experiments.

Table 8 lists the estimates of fitnesses based on the relative frequencies of fertile matings in vials, the relative mean numbers of offspring produced per fertile mating, and the product of these two components of fitness for the first, fifth (average of the fourth, fifth, and sixth), and tenth (average of the ninth and tenth) generations. The calculations for the first generation show that populations 1, 3 and 7 have essentially equal fitnesses. That is, the total numbers of offspring produced by equal numbers of pair matings of

TABLE 8

Consolidation of data on relative frequencies of fertile matings and average numbers of offspring per fertile mating into a single estimate of relative fitness. Data obtained for the first generation can be used as estimates of fitness of the experimental populations; data obtained in the fifth (average of 4th, 5th, and 6th) or tenth (average of 9th and 10th) generations apply to the present experiments only.

Generation		1	3	5	6	7	17	18	19
1	Fertility	.96	1.00	.88	.88	.94	.91	.99	1.01
	Offspring	1.02	1.00	.84	.82	1.07	.96	.91	.90
	Combined	.98	1.00	.74	.72	1.01	.87	.90	.91
5	Fertility	.97	1.00	1.14	1.14	1.19	1.17	1.20	1.19
	Offspring	.99	1.00	.82	.79	1.01	.93	.93	.85
	Combined	.96	1.00	.93	.90	1.20	1.09	1.12	1.01
10	Fertility	.97	1.00	1.08	1.07	1.12	1.09	1.08	1.11
	Offspring	.90	1.00	.83	.76	.97	.92	.92	.82
	Combined	.87	1.00	.90	.81	1.09	1.00	.99	.91

flies from these populations are about the same. This does not mean that the reproductive patterns of the populations are identical; the high productivity of fertile matings in population 7, for example, is counterbalanced by a fairly high frequency of sterile matings observed in the first generation of these tests.

The estimates of fitness of populations 5 and 6 are considerably lower than those of the preceding three populations; populations 5 and 6 produce on the average only 70–75 per cent as many offspring per mating (including sterile matings in this average) as do flies from populations 1, 3 and 7. Finally, the daughter populations of Nos. 5 and 6, which had been removed from radiation for some 40 generations, have fitnesses estimated at approximately 90 per cent; a recovery of about two-thirds of the deficit observed for Nos. 5 and 6 themselves. In the case of populations 17, 18 and 19, again, "recovery" has not proceeded along identical lines; Nos. 18 and 19, populations of some 10,000 adults, have recovered largely by the elimination of sterility, while the corresponding recovery of population 17 has been effected largely by an increase in the number of offspring produced by fertile flies.

When one inquires not about the fitnesses of the experimental populations as they exist in their population cages (estimates of which are based on the behavior of single pairs of flies in the first generation of our present experiments) but rather about the relative fitnesses of these populations under the conditions of the present experiments themselves, one obtains somewhat different estimates than those presented above. Largely as a result of the high frequency of sterile flies in populations 1 and 3, these populations give relatively low estimates of fitness at the mid-point of our experiments (generations 4, 5, and 6); four populations (7, 17, 18 and 19) exceed these populations in the total production of offspring at this time; populations 5 and 6 are nearly equal to population 1. By the end of the experiment (generations 9 and 10), further changes have occurred. Populations 7, 17 and 18 still exceed or equal the control population 3; population 1 is now exceeded by all populations but No. 6, a population which underwent a long interval of chronic gamma-radiation (2000r per generation) prior to these studies.

DISCUSSION

There is no doubt that measurements of the sort described above bear on the theoretical concept of a population's fitness. There are, however, serious problems which arise in the interpretation of the experimental data. The first of these can be described as "quantitative." How much weight should one give to the numerical values actually obtained by a given experimental technique? The viability component of an estimate of fitness, for example, is nothing more than the ratio of percentages of survival. Under different environmental conditions survival can, at least in theory, assume any value from one to zero; consequently, the ratio which measures this component of fitness can assume any value from 1/1 to 0/0. The latter is, of course, indeterminate. Granting that the populations being compared are

not identical and, therefore, that their proportions of survivors under a series of varying environmental conditions do not follow precisely the same pattern, experimental conditions may possibly be found which will give any desired numerical value of fitness. Thus, if it is known that in one environment (say, a certain degree of crowding) individuals of two populations have relative viabilities 1 : 0.95, it is quite possible that by a judicious choice of a second environment (increased crowding, for example) one can transform these values into 1 : 0.10. The results of Knight and Robertson (1957) illustrate this type of phenomenon; a comparison of values obtained in the present experiments with those reported earlier (Wallace, 1956) reveals the same point. The numerical values which may be obtained experimentally do not, in themselves, offer any basis for deciding which technique is "correct"; this decision rests on a proper understanding of the relationship between various possible experimental techniques and the situations which commonly prevail within the populations being studied.

The second problem which arises in this type of investigation may be described loosely as "qualitative." Quantitatively, we were concerned with deciding which of several estimates of fitness is most meaningful; we assumed, however, that all estimates agreed as to direction and varied in magnitude only. Qualitatively, we are concerned with fluctuations in estimates which are real (as opposed to sampling or experimental errors) and which indicate that the fitnesses of two populations under different circumstances may have their relative standings reversed. The mere fact that sterile flies are frequently highly viable indicates that complications of this sort are to be expected. It is quite possible that qualitative complications of this sort are those which are responsible for the genetic diversity of populations and, at least in part, for the retention of genetic variation within local populations (da Cunha et al., 1950). These complications introduce an element of uncertainty into any experimental study of fitness which fails to include all components of fitness, which exaggerates the relative importance of any single component, or which includes environmental conditions differing from those in which one's interest really lies. The data presented in table 7 revealed that the small numbers of flies representing the competing populations frequently reversed their relative standings in successive generations. The information given in table 8 indicates that populations reverse their relative positions in respect to frequencies of fertile flies and the average number of offspring produced by fertile pairs. Furthermore, average estimates of fitness for the same population changed markedly during the course of the generations, as both tables 6 and 8 show. The estimate of relative fitness of population 7 determined in the early generations of the vial tests differs considerably from that yielded by earlier tests limited to the second chromosome alone. The genetic tests based on the relative viabilities of CyL/+ and +/+ flies in half-pint culture gave 0.97–0.99 as an estimate of fitness for population 7 (see Wallace, 1956); a later test (unpublished data) based on cultures yielding four classes of flies gave a somewhat lower estimate; the experiments reported in the present

paper give 1.07 and .94 as two estimates based on two different components of fitness. Complications of a similar sort frequently arise from attempts to incorporate longevity as one of the measurable components of fitness. It sometimes happens (see Wallace, 1948, for example) that the variance of mortality for individuals of one population exceeds that of individuals from a second source. Even though the mean life span of the individuals from the first population may be lower than that of the second, there exists a time when the number of survivors of this group exceeds that of the second. Haldane's (1932) demonstration that intense selective pressures favor the more variable population of individuals rather than the population with the greater mean applies to this type of situation.

The variations which one can observe in estimations of fitness—variations resulting from novel gene combinations, from differences in environmental conditions under which the tests were made, and from the inclusion of different components of fitness in different tests—can be overcome statistically so that a highly accurate estimate of an average fitness can be obtained for a population under a given set of environmental conditions. One should, however, bear in mind the magnitude of the variance of different estimates found under a variety of conditions, for in many instances the future of a population will depend upon its fitness at a given time; mean values and errors of these means are not sufficient to anticipate these times of crisis nor to predict the course of selection at these times. Penrose (1949) has emphasized a rather similar point. He points out that in human populations the ratio of the number of mature daughters to the numbers of their mothers is a measure of fitness; at different times in one population and in different populations this measure varies tremendously.

Regarding the genetic effects of radiation on populations, the data presented above add to the information previously available. First, they have magnified many of the differences previously noted between irradiated and control populations. Where the second-chromosome tests, which were limited primarily to relative viabilities of larvae in half-pint cultures, had led to estimates of fitness between 0.92 and 0.98 for populations 5 and 6 (depending upon the population and the time the tests were made—see Wallace, 1956), the present tests give overall estimates (production of offspring combined with percentage fertile matings) in the low 0.70's. Second, they have indicated very strongly that population size is intimately associated with the extent to which mutant genes (including induced mutations) can be utilized on the basis of their behavior in heterozygous condition. Third, they have shown that chance events can bring about fluctuations in fitness of the experimental flies larger, for instance, than the mean effect of exposure of a Drosophila population to 300r per generation. The latter effect is not mentioned in an effort to have chance fluctuations join radium-dialed wrist watches as a pseudo-justification for subjecting populations to radiation. It is mentioned because to many persons the fitness of a population represents a biological constant comparable to the pH of blood; such a view of populations is highly erroneous.

SUMMARY

This paper deals with an attempt to estimate the relative fitnesses of several experimental populations of *D. melanogaster*. The measure of fitness used was the number of offspring produced by single pairs of individuals. Each experiment consisted of a study of two "competing" populations. Fifty males and 50 virgin females from each of two populations were mated as single pairs in vials. The number of sterile matings was recorded; the offspring produced by fertile pairs were counted fourteen days after mating. Males and virgin females were collected from these vials to establish a second generation of 50 single pairs in vials. The experiments were continued in this way for ten generations. All possible pairs of eight populations (see table 1) were studied.

Among the flies representing populations 1 and 3, frequencies of sterile matings increased in successive generations to a high level; this increase must be ascribed to selection of sterility genes in heterozygous condition. In contrast with the increase observed in populations 1 and 3, the frequency of sterile matings decreased in populations 5, 6 and 7. In the remaining three populations (Nos. 17, 18 and 19) the frequency of sterile matings was constant at a relatively low level.

Two of the experimental populations (Nos. 1 and 7) produced more offspring per *fertile* mating in the first generation than did the control population (No. 3). However, every large, irradiated population suffered a progressive decline in the relative numbers of offspring produced per fertile mating in successive generations under the conditions of these studies. Three populations (Nos. 5, 17 and 18) did not show this decline; these either are small populations or have been derived from a small population. This is interpreted as the effect of an abrupt change in population size on fitness. It is also regarded as further evidence for the retention of genes in large populations on the basis of their action in heterozygous condition.

Estimates of fitness varied among different samples of flies taken from the same population, among different generations of the same sample, between the two components under observation (fertility and number of offspring produced), and at different times during the course of these experiments. The fitness of a population is not a constant which can be measured, recorded, and then referred to when occasion demands.

These results and the difficulties encountered in interpreting such information are discussed.

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SOME EFFECTS OF SECONDARY DISPERSIVE PROCESSES ON DISTRIBUTION

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The mechanisms by which animals are dispersed among localities are frequently different from those by which the same animals move within one locality. The distinction is a commonplace one and has been discussed in a number of papers. Long-distance dispersal, whether it be active or passive, is almost always confined to one or a few seasons of the year and stages of the animal's life history. Local dispersal may not be so confined.

I shall call dispersal within locality "secondary," and I shall regard locality as that space within which there is a high probability of re-establishment between generations and hence a high biological continuity. The size of a locality is thus a species-specific statistic which depends on the mobility of the animal; that is, the relative probability of its various mechanisms of movement.

One general finding of the recent very active work in sampling of small animal populations has been that most distributions of small animals are highly contagious. The distributions of many populations have been shown to be well described by the negative binomial. In this distribution the statistic K is a measure of the degree of aggregation. This statistic varies with aggregation, density, sample size, and size of the sample unit (Waters and Henson, 1959). With proper control of sampling technique, however, K may be considered to be an expression of the degree of aggregation. In distributions with zero and one counts only, K will be indeterminate. As multiple counts appear, K assumes a finite value which may be used directly as an expression of aggregation even if the distribution examined does not show a good negative binomial fit. The computation of K may be done conveniently by two methods described by Anscomb (1949). The choice of method depends on the level of a preliminary estimate of the statistic. It is made with the view of providing maximum efficiency.

Three biological parameters will determine the distribution within locality of an animal which is dispersed at only one stage of its life history and at one time of year. The first of these is the physical structure of the substrate; second, the response of the dispersing animals to the physical gradients and other stimuli within the substrate; and third, the distribution of mortality which intervenes between the establishment of the animals and the time at which their distribution is observed.

Phyllocnistis populiella Chamb. is a leaf miner on poplar. It is dispersed only at the adult stage of its life history. Eggs are laid on leaves of opening buds; larvae are apodous and establish a single tortuous mine within the epidermis of the leaf. The leaves are not killed or even seriously injured

TABLE 1

Frequency distributions of *Phyllocnistis populiella* Chamb.
Kootenay Crossing, B. C., 1956 to 1958
(N = 240 terminals)

Year	Larvae per terminal							K
	0	1	2	3	4	5	6	
1956	234	6	0	0	0	0	0	Indeterminate
1957	224	11	4	0	0	0	0	0.17
1958	151	61	20	6	1	1	0	1.67

(Needham, Frost and Tothill, 1928). Each leaf will usually support only one larva to maturity. A number of mines may appear on the leaves of a single terminal. In table 1, frequency distributions of larvae per terminal (4.5 leaves: Henson, 1954) are given for three successive years during the growth of a population. K values for each of these distributions are computed. Sampling was done soon after the establishment of the mines.

The population represented in table 1 increased twenty-fold from the time of its appearance in 1956. During this increase and following the establishment of multiple counts, the K increased ten-fold. Each distribution appears to be an intensification of the one preceding it. Apparently each of these distributions has resulted from identical behavior on the part of increasing numbers of adults.

The mortality which occurs during the course of a generation's feeding from the establishment of the mine to the time of pupation is illustrated in table 2. Frequency distributions from four weekly samplings of the same population together with computed K values are given.

The mortality for the period amounted to some 57 per cent of the initial population. This was concentrated in the multiple infestations, and the value of K increased as the result of the increasing preponderance of one-counts.

Quite a different picture is presented by the distribution of galls of an undescribed Eriophid mite (Felt, 1940). Frequency distributions for a population of these mites during a period of increasing population are presented in table 3. K values for each distribution are computed as before.

TABLE 2

Frequency distributions of *Phyllocnistis populiella* Chamb.
McLeod, B. C., 1958
(N = 240 terminals)

Week	Larvae per terminal						K
	0	1	2	3	4	5	
1	213	22	2	2	1	0	0.27
2	218	20	1	1	0	0	0.56
3	223	16	1	0	0	0	2.00
4	225	15	0	0	0	0	Indeterminate

TABLE 3

Frequency distributions of Eriophyes galls. Great Divide, B. C., 1956 to 1959 (N = 240)

Year	Galls per terminal													K
	0	1	2	3	4	5	6	7	8	9	10	11	12	
1956	224	11	4	1	0	0	0	0	0	0	0	0	0	0.13
1957	225	8	4	0	1	1	1	0	0	0	0	0	0	0.05
1958	132	39	17	10	13	9	4	4	4	3	2	2	1	0.36

During the three years of the sampling the population increased roughly fifteen-fold, and in contrast to the behavior of the Phyllocnistis population the degree of aggregation remained rather low. In other words, as the population increased, it dispersed within the locality at the same time. The best evidence of this is to be found in the great reduction of zero counts and the rather even increase in the number of counts greater than one. All these sampling results apply to early season populations. Since Eriophyes continues to breed throughout the summer (Essig, 1958) it is common to find the

TABLE 4

Frequency distributions of Eriophyes galls. Baker Creek, Alta., 1958

Time	Galls per terminal													K
	0	1	2	3	4	5	6	7	8	9	10	11	12	
Spring N = 450	271	76	33	20*	20	14	5	7	3	1	0	0	0	0.40
Summer N = 379	184	70	43	22	23	8	10	9	4	4	1	1	1	0.55

numbers of galls increasing through the course of the season. Frequency distributions of a spring and a summer sampling of the same population are given in table 4. In this table, the total number of counts does not remain the same as in the previous data. K values are given as before.

The increasing population illustrated in table 4 shows no marked change in its aggregation. This is in sharp distinction to the behavior of the population illustrated in table 2. The nature of the increase in Eriophyes populations may be suggested by an examination of the number of uninfested ter-

TABLE 5

Frequency distributions of successive zero counts of Eriophyes (populations from table 4)

	Number of successive zero counts														
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Spring	69	32	30	14	11	5	4	2	6	2	2	2	1	1	0
Summer	31	33	6	14	6	4	4	4	5	2	1	1	1	1	0

minals surrounding an infested one. This statistic is a measure of clumping. Distributions of consecutive negative counts for the spring and summer populations are presented in table 5.

It will be seen at once that the main difference between the two populations is that there were many more adjacent terminals infested in the higher summer population. This strongly suggests that the increase in gall numbers was accompanied by a movement from infested terminals to adjacent uninfested terminals.

We have then, two situations which appear to be rather different. The Phyllocnistis infestation is established each season by a dispersive mechanism operating during the short period of adult activity. Mortality is concentrated in such a way that it tends to mediate against multiple infestation of a terminal. An increase in overall density is accomplished by an intensification of the pattern of distribution and a consequent intensification of aggregation. This leads to the differential mortality within the intensified aggregations.

In contrast, the Eriophyes populations appear to be established each season through the operation of a dispersive mechanism, but modified during the season by a dispersive mechanism which mediates against the intensification of aggregation with increasing density. The increase in Eriophyes during the season is accompanied by very short-distance movements which preserve the physical nature of the aggregations but enlarge them. This is accomplished by simultaneously increasing the intensity of infestation on previously occupied terminals and by involving adjacent terminals. There is no apparent overall shift of the population or adjustment of the nature of its aggregation.

These two examples suggest that the manner in which the substrate is utilized may be in part a function of secondary dispersal. Apparently, Eriophyes has the ability to modify its pattern of secondary dispersal in response to density. The mechanism appears to operate only at the time of initial establishment of a season's brood. During subsequent breeding, establishment of the brood is accomplished with minimum movement and without respect to density.

Phyllocnistis appears to have a rather rigid dispersive mechanism which is not modified as a response to density. Changes in its distribution during the course of a generation are accomplished by differential mortality. Waters and Henson (1959) found such a wide variability in the aggregation of the populations which they examined that the behavior of Phyllocnistis appears unusual.

The degree to which the substrate can be utilized may be partly a function of the flexibility of the dispersive mechanisms within the locality. I expect that animals which are able to exhaust their substrate will always prove to be very mobile at some period of their life histories, and that they will always show some modification of behavior which is mediated by population density. Recent work on parasitic insects by Burnett (1958a, b, c) might be interpreted to support this view. Animals which have rigidly de-

termined dispersive mechanisms may not in general be able to exhaust their substrate, because the attrition of mutual interference between individuals within progressively intensified aggregations will limit the populations before these aggregations can involve a critical proportion of the substrate. The density at which such an effect would intervene should be a function of the degree of aggregation. The most markedly aggregated species would be limited at the lowest overall densities.

Animals which are able to decrease the degree of aggregation as density increases through a modification of their secondary dispersive mechanisms should be able to reach high densities and to utilize a large part of the substrate. It may be that the capacity for density-stimulated modification of the secondary dispersive processes affecting "within-locality" movements is one important difference between insects which reach intolerable densities and those which always seem to regulate at tolerable levels.

SUMMARY

The ability of an animal to modify its dispersive mechanisms as a response to density appears to vary among species to some extent. This ability may be critical in providing a means whereby aggregative tendencies may be reduced as overall density increases. Without such a reduction, mutual interference between individuals within an aggregation may well limit a population at rather low overall densities.

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ON THE ANOMALOUS RESPONSE OF *DROSOPHILA PSEUDOOBSCURA* TO LIGHT

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In a recent paper on the behavior of a number of species of Drosophila, Pittendrigh (1958) reported that *D. pseudoobscura* exhibited a clear *negative* phototaxis, and indeed the data presented by Pittendrigh (reproduced as figure 1 of the present paper) are striking. These results are quite surprising inasmuch as it is the common experience of geneticists who work with *D. pseudoobscura* that this species usually exhibits a strong *positive* reaction to light. Two sorts of observations which are common in the laboratory will illustrate the point. First, if in the course of transferring flies from one bottle to another a few flies should escape, or if the plug should fall out of a culture bottle, the escaped flies immediately make for the nearest window during daylight hours but not at night.

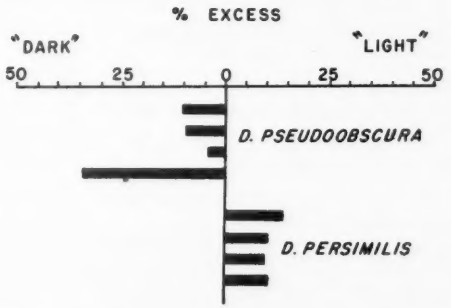

FIGURE 1. Results of tests made by Pittendrigh on four strains of *D. pseudoobscura* and *D. persimilis*. Flies were released into a blackened Y-tube with light of different intensities illuminating opposite arms. Plotted are the excesses above 50 per cent of the tested individuals entering the darker or lighter arm. Adapted from Pittendrigh (1958).

Second, a common method of changing population cages of *D. pseudoobscura* makes use of their photo-positive response. The cage in which the flies are is covered with paper or opaque cloth, the clean cage is attached to the old one, and a light source is placed near the clean one at a point opposite to the attachment of the cages. If the old cage is struck several sharp blows with the fist, the flies stream out of the old cage into the clean one, piling up at the illuminated end. Nearly all the flies can be transferred from one cage to another by this method.

In view of these observations and a number of other similar experiences in my laboratory and in others, it seemed worthwhile to investigate the behavior of this species in somewhat greater detail.

EXPERIMENTAL METHODS

The experimental methods used were of the crudest sort, but as the results show these were quite refined enough for the purposes of the experiment. The three pieces of apparatus used, Y-tube, glass cylinder, and bell jar, were placed approximately four feet from a large window measuring approximately seven by four feet, the only source of illumination in the room. All experiments were performed on a series of uniformly overcast days between 9:30 A.M. and 3 P.M. Readings with a Weston exposure meter showed

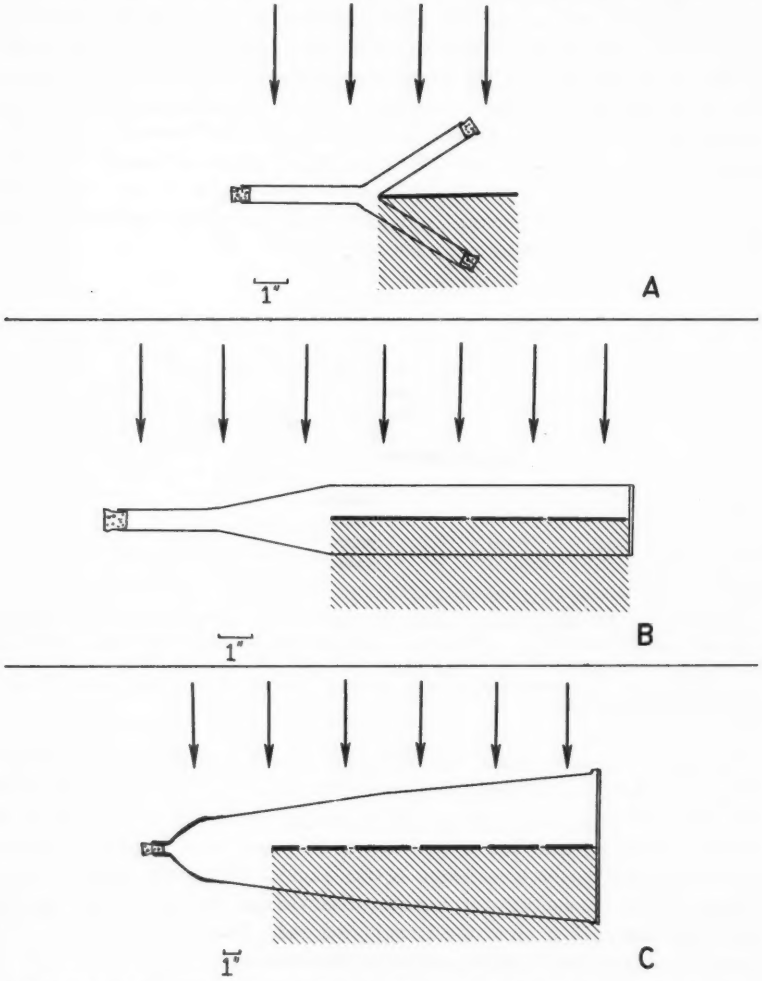

FIGURE 2. Y-tube (A), glass cylinder (B), and bell jar (C) used in the present experiments. Arrows indicate the direction from which the illumination came; shading shows the darker side of each apparatus. Scale at the lower left of each figure.

a uniform light intensity during the experiment of 12–14 scale units on the light side of each apparatus and 0.2 to 0.3 on the dark or shaded side. These latter readings are close to the limit of detection of the meter. Figure 2 shows each piece of apparatus in position for the experiment. The Y-tube in figure 2a was placed so that one arm was in the shade of an opaque partition of corrugated paper, and one in the light, the entrance arm being uniformly illuminated from the light side. In both the glass cylinder shown in figure 2b and the bell jar in figure 2c, the partition of corrugated paper was so constructed that flies could walk from one side of the partition to the other at intervals along the length of the apparatus and at either end of the container.

Flies for the experiments were transferred from culture bottles to empty glass containers and allowed to sit in these containers for 10–20 minutes before use. Because of the high humidity in the culture bottles, freshly removed flies showed very little mobility and a general inability to maintain their balance. After 10–20 minutes in a dry bottle, however, the flies were able to walk or fly easily. All individuals were transferred from storage bottles to the experimental apparatus by an aspirator so that no tested individual had ever been etherized.

EXPERIMENTS IN Y-TUBES

a) *Y-tube prone, single flies*

Flies were introduced singly into the Y-tube, shaken down to the cork at the end of the entrance tube, and the Y-tube quickly placed in the position shown in figure 2a. Each individual was run twice, the tube being rotated 180° between runs so that inherent differences in the tube and possible olfactory tracks produced by the flies would not bias the experiment. A fly was scored after it had walked half way down either arm of the tube. After each fly had completed its two runs it was released before the next fly was introduced into the tube. The results of 20 runs with males and 20 with females are given in table 1. They are in complete accord with those of Pittendrigh. The flies indeed demonstrate a strong avoidance of the light under these conditions.

TABLE 1

Number of choices of light or dark made by flies in Y-tube experiments

Experiment	Males			Females		
	Light	Dark	No choice	Light	Dark	No choice
a. Single flies tube horizontal	2	18	...	5	15	...
b. Ten flies tube horizontal	1	15	4	0	15	5
c. Single flies tube vertical	11	9	0	11	9	0
d. Ten flies tube vertical	8	11	1	10	8	2

b) *Y-tube prone, ten flies*

A group of ten flies was introduced into the tube, shaken down to the cork of the entrance tube, and the apparatus put in place. Each group of ten flies was run twice, the tube having been rotated 180° between runs. It was not possible to observe the choice of each fly as in the previous experiment since there was a considerable amount of milling about on the part of the flies, apparently excited by close proximity to each other. Each run was then allowed to go on for five minutes, at the end of which time the flies had come to rest so that the number of individuals in each arm of the tube could be counted. Table 1 shows the results of two runs for males and two for females. Again there is strong negative phototaxis shown. However, it was noticed that many flies went initially to the light side and then walked back to the dark side, some flies changing position several times during the waiting period. This suggested that the level of excitement of the flies might affect their response, and this observation led to the succeeding experiments.

c and d) *Y-tube upright, single flies* (c) *and ten flies* (d)

Experiments c and d were identical with a and b except that the Y-tube was kept in an upright position, so that the negative geotaxis of the flies increased their rate of movement. Table 1 shows the results of these experiments. The situation here is quite different from the results of experiments a and b. The flies have lost their negative phototactic response and show approximately equal propensities for light and dark sides of the tube. There is a slight suspicion, though not significant, of a preference for the light.

GLASS CYLINDER EXPERIMENTS

In the glass cylinder apparatus shown in figure 2b, the flies were forced to walk into the main chamber through the long narrow entrance tube. Once they had passed the neck of the cylinder, however, they were free to fly, a condition not possible in the Y-tube.

e) *Single flies—walking*

If flies are introduced singly into the neck of the glass cylinder, and the cylinder is not disturbed, only walking behavior is manifested with the re-

TABLE 2

Number of choices of light or dark made by flies in glass cylinder experiments

Experiment	Males			Females		
	Light	Dark	No choice	Light	Dark	No choice
e. Single flies walking	0	20	...	1	19	...
f. Ten flies walking	...	...	...	1	19	0

sults shown in table 2. Again the flies are strongly photonegative. Thus in a container with a volume forty times that of the Y-tube, the response of walking flies is the same.

f) *Ten flies—walking*

Four runs of ten flies each are shown in table 2. As for the Y-tube experiments, the numbers of flies in light and dark side are those after five minutes of equilibration time.

g) *Fifty flies—agitated*

In this experiment 25 males and 25 females were introduced into the cylinder, shaken down onto the entrance cork and allowed to move back into the body of the cylinder. During the initial period of movement the cylinder was agitated by rapping it sharply against the table on which it rested.

TABLE 3

Number of flies in light or dark side of glass cylinder at various times after agitation of the vessel. 25 males and 25 females mixed

Time	Run 1		Run 2		Total	
	Light	Dark	Light	Dark	Light	Dark
0	42	8	36	14	78	22
1 min.	23	27	20	30	43	57
2 min.	18	32	17	33	35	65
3 min.	16	34	14	36	30	70
4 min.	13	37	13	37	26	74
5 min.	13	37	11	39	24	76
6 min.	13	37	11	39	24	76
7 min.	13	37	11	39	24	76

This was continued until all the flies had left the entrance tube. During the constant agitation period most of the flies flew rather than walked into the body of the cylinder, and as soon as the last fly had left the entrance tube a count was made of the numbers on each side of the barrier. Thereafter counts were made every minute in the absence of any external agitation, with the results shown in table 3. Obviously individuals flew to the light, but as their level of activity went down they walked back into the dark. After five minutes of equilibration all of the flies had ceased movement and were stationary at various places on the corrugated partition or, more rarely on the glass.

BELL JAR EXPERIMENTS

While many flies were observed to fly into the glass cylinder in experiment g, it was not possible to estimate how much the flight reaction was responsible for the positive phototaxis seen. As a final experiment, then, the large bell jar shown in figure 2c was used. As a control, flies were

introduced singly into the bell jar in such a way that they walked along the short entrance neck and onto the inner surface of the jar. Any fly which showed some flight reaction, no matter how short, was not counted. Table 4 shows that the result is indistinguishable from that of the Y-tube experiment. In a second set of trials a narrow tube was inserted into the bell jar so that its inner opening projected about two inches into the main chamber. Single flies entering this jar were forced to fly out of the end of the tube into the bell jar, with the results shown in the right-hand side of table 4. The contrast between the negative phototaxis when walking and the positive phototaxis when flying is apparent from the table.

TABLE 4

Number of choices of light or dark made by flies in bell jar experiments. Flies released singly

Experiment	Males		Females	
	Light	Dark	Light	Dark
Walking	5	15	3	17
Flying	14	6	16	4

All of these experiments suggested that the observations of the behavior of flies in population cages mentioned earlier were incomplete, and that although flies could be induced to go from one cage to another by agitating them and attracting them by light, there ought to be a reverse movement after a short time of no disturbance. To check this, about 180 flies were introduced into a clean plastic population cage which was marked off along its length into eight equal zones. The cage used is a rectangular transparent lucite box approximately 18" × 4" × 5". The cage was oriented with its long axis at right angles to the plane of the window, and the flies were introduced into the cage at the end opposite to that of the light source. It should be noted that there were no partitions in the cage, so that the contrast between "light" side and "dark" did not exist as in the other experiments. What is measured is the movement of the flies toward or away from the light source. As the flies were introduced the cage was agitated by rapping it against the table. In this initial period three counts were made of the flies in each zone, during which time there was considerable movement to and fro in the cage. Some flies were in flight and could not be counted, and the great pile-up of flies at the light end (zone 8) made it impossible to count the flies in that region. It should also be noted that zones 1 and 8, being at the ends of the cage, have an extra surface for flies to accumulate on. In table 5, the number in zone 8 has been estimated for the initial period by subtracting the sum of the other zones from the total found in later periods. At three-minute intervals, without agitation, the flies in each zone were counted again with the results shown in table 5.

TABLE 5

Number of flies in each zone of plastic population cage at various times after release into the cage. Zone 1 is farthest from the light, zone 8 closest

Time	Zone							
	1	2	3	4	5	6	7	8
	"Dark" end							"Light" end
0	15	5	6	11	7	9	4	96 (est.)
0	16	7	7	8	7	4	9	95 (est.)
0	13	4	6	8	7	6	6	104 (est.)
3 min.	55	8	8	6	3	5	6	66
6 min.	75	14	4	4	4	5	5	43
9 min.	87	8	5	5	3	3	5	33

Again it is confirmed that when flying or walking at a high rate of excitation the flies are *positively* phototactic, while at lower levels of excitement the phototaxis is reversed.

DISCUSSION

The experiments described show that *D. pseudoobscura* is not an exception to the general positive phototaxis of Drosophila except at low levels of excitation. The origin of the positive phototaxis of Drosophila cannot be properly discussed in the absence of more detailed knowledge of their ecology. Positive phototaxis at high activity levels may be an escape reaction, but since the predators of Drosophila are in general unknown nothing definite can be said. The reversal of the usual positive phototaxis at low levels of activity in *D. pseudoobscura* may very likely be an adaptation to life in dry environments, as suggested by Pittendrigh. Dark places such as the undersides of fallen leaves, interstices of decaying logs and similar habitats are generally moister than open and more insolated spots. In this connection it is relevant that the closely related species *D. persimilis*, which lives in moister, cooler climates, was found to be photo-positive by Pittendrigh at low activity levels. As always, however, explanations of such observations as specifically adaptive must remain *ex post facto* rationalizations.

SUMMARY

Under usual conditions of handling in the laboratory, *D. pseudoobscura* shows a number of evidences of positive phototaxis. In an experiment to determine the reaction of this species to light, Pittendrigh (1958) found them to be negatively phototactic in contrast to general observation. The experiments reported in the present paper show that *D. pseudoobscura* is indeed negatively phototactic under conditions of low excitement, but that if the flies are forced to walk rapidly or to fly, they lose their negative phototaxis and become strongly attracted to light.

LITERATURE CITED

Pittendrigh, Colin, 1958, Adaptation, natural selection and behavior. *In* Behavior and evolution (Anne Roe and G. G. Simpson, Eds.). Yale University Press, New Haven, Connecticut.

LETTERS TO THE EDITORS

Correspondents alone are responsible for statements and opinions expressed. Letters are dated when received in the editorial office.

THE NATURE OF THE "PEARL" MUTATION IN *TRIBOLIUM CASTANEUM* HERBST

Park (1937) discovered a mutation (pearl) which affects the compound eye of the tenebrionid flour beetle *Tribolium castaneum*. In the normal beetles the eyes are characteristically black. In the pearl mutant, only the peripheral facets are black, and the middle facets appear devoid of pigment. His genetic crosses showed that the pearl eye is the result of the action of an autosomal recessive gene.

Since histological preparations had not been prepared, Park was not able to tell whether (1) the entire eye was affected, or whether (2) only the pigment was lacking from the abnormal eyes.

Recently the eye in normal and pearl beetles has been examined from the medial side. The beetle is placed in a drop of glycerine and decapitated. Using jeweler's forceps the head is broken along the mid-line, and the brownish-red exoskeleton surrounding the eye is chipped away. Tissues medial to the retinula are removed, exposing it in its entirety. The eye is transferred (retinula side up) to a small drop of glycerine on a clean slide and covered.

Although the inner surface of the head at the eye is deeply concave, the medial surface of the retinula is much less so. Hence, it is possible to draw its outline with the aid of a camera lucida. The results are shown in figure 1.

In the figure the retinula of the normal eye is shown at left (A). It consists of a solid black membrane, broadest next to the ventral side of the

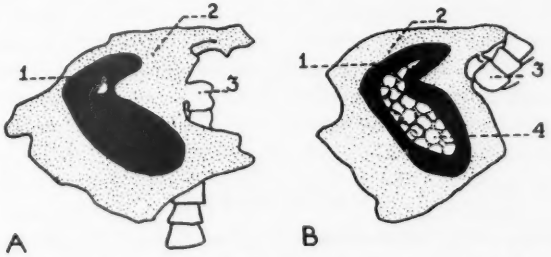

FIGURE 1. The medial aspect of the retinula in normal *Tribolium castaneum* (A) and in the pearl mutant (B). 1 = retinula; 2 = inner surface of head exoskeleton; 3 = basal segment of antenna; 4 = outline of eye facet. (× 100)

head, somewhat less so next to the lateral part of the head, and tapering to a blunt end as the retinula progresses dorso-antero-medially under the eye.

The retinula of the pearl eye (B in the figure) has roughly the same shape. In contrast with the normal eye, however, it has a clear space in the middle. Through the transparent tissue filling the space between the retinula and the exoskeleton it is possible to make out the outlines of the facets.

Thus, it is evident that the pearl gene prevents the complete formation of the retinula. The color of the eye (in normal Tribolium at least) is probably due to the black retinula, although in the normal eye the ommatidia are known to possess pigment granules. In the pearl mutant, when the eye is examined from the outside, only the facets on the periphery lie over the retinula and thus appear pigmented. If the ommatidia in the clear area are normal the pigment granules must be very small, since the facets appear clear. Histological sections of the eyes of late larvae, pupae and young imagoes are being prepared to determine whether the gene affects the ommatidia.

It is of interest that the pearl gene, *p*, also affects the juvenile stages. As early as the first instar it is possible to differentiate between genetically *p*/*p*, +/*p* and +/+. The few larval ocelli in the latter are distinct black dots; in the pearl larvae no ocelli are visible either because they are not pigmented or because they are absent. (Histological examination should clear this point.)

The +/+ or +/*p* pupa can be recognized soon after the ommatidia begin to develop, since they are pigmented and present throughout the eye. With further development the whole eye in the pupa becomes brown, and in a very late pupa the eye is completely black. Thus the +/+ or +/*p* imago hatches with perfectly developed black eyes.

In the pearl pupa's eye fewer ommatidia are observable, only in the periphery of the eye, and only at a late stage of development. The retinula develops only under the peripheral facets in the late pupa. The retinula in a freshly emerged imago is very narrow and greyish in color. As the beetle ages, more retinula is formed (and becomes black in color), but it does not develop completely.

In summary, the pearl gene in *Tribolium castaneum*, so far as known, appears to have the following effects: (1) lowering of productivity of pearl eyed females (Park, 1937); (2) elimination of pigment in the larval ocelli; (3) delay in appearance of the ommatidia in the pupa; (4) decrease in the amount of substance from which the retinula is formed; (5) delay in the formation of the retinula.

ACKNOWLEDGMENTS

The author is obligated to Professor Thomas Park, Department of Zoology, University of Chicago, for providing the Tribolium wild type and pearl stocks. The hospitality of the Biological Laboratory, Cold Spring Harbor,

New York, through the courtesy of Dr. M. Demerec, is greatly appreciated. This investigation was supported, in part, by a grant (G-4501) from the National Science Foundation.

LITERATURE CITED

Park, Thomas, 1937, The inheritance of the mutation "pearl" in the flour beetle, *Tribolium castaneum* Herbst. Amer. Nat. 71: 143–157.

ALEXANDER SOKOLOFF

BIOLOGICAL LABORATORY
COLD SPRING HARBOR, NEW YORK*

April 7, 1959

*Present address: The William H. Miner Agricultural Research Institute, Chazy, New York.

THE ROLE OF SEXUAL ACTIVITY IN HUMAN SOCIETY

The paper by G. E. Hutchinson, "A speculative consideration of certain possible forms of sexual selection in man," in the March–April, 1959, issue of *The American Naturalist* is a welcome contribution to a subject of great interest and importance. It is a pleasure to read a well balanced and relaxed treatment of a topic which is usually approached with parataxic tension.

However, Hutchinson ignores one point, a consideration of which may clarify the problem to some extent. He never raises the question of the function of sexual activity in human society; he seems tacitly to assume that it is solely reproductive. He defines paraphilia as "a tendency to substitute, in... sexual behavior, goals which cannot lead to reproduction." Hence paraphilia is an anomaly which needs explanation.

Obviously, reproduction is one of the functions of human sexual activity, but, viewed realistically, it is certainly not the only one. A small fraction of the sexual activity of the species would satisfy reproductive needs. For the individual, sexual activity is a recreational, tension-releasing, euphoria-producing process. Socially, it is a ubiquitous force producing solidarity and integration. Not all sexual activity is genital and climactic. Mild sexual advance and response occur repeatedly in human society without leading to climax. The casual wolf whistle evoked by an attractive girl, a dancing couple, a kidding conversation with a waitress are not all cases of frustrated seduction. All societies channel climactic sex within limits even though the rules are sometimes broken. But all of them also recognize appropriate expressions of subclimactic sex; these give gratification to the participants, help keep society going and are an important function of sex.

In our society there are homosexual as well as heterosexual instances of subclimactic sex. The warm handshake, the camaraderie of the locker room,

kisses exchanged between women friends, the admiration of athletes are clearly of this sort. Sometimes these mild expressions spill over into climactic activity. In our culture they do so only in opposition to intense social pressure; in other cultures such transgressions may be ignored, condoned or actually structured. But whatever the degree of overtness, homosexual elements are present and also perform a function. They probably contribute greatly to the mitigation of inter-male and inter-female rivalry and aggression. Other forms of paraphilia can also be better understood in the context of the functions of sexual activity than as mere aberrations from an absolute.

One problem, as Hutchinson states, is to what degree does non-reproductive sexual activity produce differential fecundity among individuals and how does this affect selective forces. But viewed in the light of the broader function of sex, the subsidiary problem becomes what produces the extreme variants—not why does non-reproductive sex exist. Are these variants the extreme genotypes which must be produced in every generation in order to preserve the complex genetic system responsible for the modal phenotype? Hutchinson does not pretend to have the answer to this question, nor do we, and we heartily second his motion that the subject receive further thought and research. It is a particularly difficult field not only because the processes involved are highly complex but also because it arouses emotions which distort thinking and bury facts. There can be no doubt that the revulsion that most people feel toward climactic homosexual practices makes it almost impossible to get at the facts. It certainly obscures the continuum which exists between the exclusively heterosexual and the extreme homosexual. Even available information must be cited with the greatest caution to avoid injuring one's informants. But perhaps perseverence in an honest endeavor to understand things as they are may eventually lead us somewhere.

L. CLOVIS HIRNING
R. R. 1, KATONAH, N. Y.

JAMES C. KING,
DEPARTMENT OF ZOOLOGY
COLUMBIA UNIVERSITY
NEW YORK, N. Y.

April 22, 1959

I am grateful to Dr. Hirning and Dr. King for their appreciative comments, and regret if I appear to assume that the function of sexual activity in man is solely reproductive. I agree with the general position that the writers take in their comment. When, however, one is dealing with the distribution of hypothetical genotypes, the reproductive aspects are obviously paramount; however, many important non-reproductive aspects may exist.

G. E. HUTCHINSON

YALE UNIVERSITY
NEW HAVEN, CONNECTICUT

April 29, 1959

THE AMERICAN SOCIETY OF NATURALISTS

SECRETARY'S REPORT

The annual business meeting of the Society was held in Washington, D. C., at the Shoreham Hotel on December 30, 1958, with President G. Evelyn Hutchinson presiding.

The minutes of the last meeting were accepted as published.

The report of the Nominating Committee (LaMont C. Cole, Chairman; Paul L. Errington, and Thomas Park) was presented by the Secretary. With no further nominations from the floor, the following officers were elected unanimously:

President (1959): Paul B. Sears
Vice President (1959): Arthur Hasler
Secretary (1959-1961): Earl Green

A motion was made and passed that the time and place of the 1959 meeting of the Society be left to the discretion of the incoming officers and the Executive Committee and that the members of the Society be notified of this decision at the earliest convenient date.

Upon recommendation of the Executive Committee, Dr. Alexander Petrunkevitch was elected an Honorary Member of the Society.

Fifty-seven persons, nominated by members of the Society and approved by the Executive Committee, were elected to membership. Names of those who have accepted membership as of February 27, 1959, are as follows:

Philip H. Abelson	James A. Jenkins	M. T. M. Rizki
A. Earl Bell	Oscar Kempthorne	Howard A. Schneiderman
Jane V. Brower	John Keosian	John R. Shaver
Lincoln P. Brower	Philip Levine	Robert R. Sokal
John H. D. Bryan	Margaret Lieb	Erich Steiner
A. B. Burdick	Robert H. MacArthur	Harry T. Stinson, Jr.
Arthur Chovnick	Betty C. Moore	Lewis W. Taylor
George L. Church	D. R. Parker	E. Peter Volpe
Sheila Counce	David Pimentel	R. C. von Borstel
Ingrith J. Deyrup	Thad Pittenger	Henry A. Wallace
Milton Fingerman	Henry L. Plaine	Ernest E. Williams
Stanley M. Gartler	Kenneth S. Rawson	

The Treasurer's Report was read and accepted.

The report of the Editor, The American Naturalist, was read by the Secretary and accepted. The Executive Committee, in consultation with Professor L. C. Dunn, appointed the following persons to the Editorial Board (Class of 1961):

Barry Commoner	S. E. Luria
C. B. Van Niel	Walter Landauer

The Secretary reported that during the past year five members of the Society died while ten resigned their membership. Those who died during the year were Ernst Artschwaeger, Richard B. Goldschmidt, Lewis Knudsen, K. S. Lashley, and Arlow B. Stout. Those who resigned were Dean Amadon, Min-Chuh Chang, Adreance S. Foster, Felix G. Gustafson, Francis O. Schmitt, Irwing W. Bailey, Graham P. Dushane, Thomas H. Goodspeed, Kieth R. Porter, and Folke K. Skoog.

At the annual meeting in 1957 held at Stanford, a motion was made and passed that the President appoint a committee to consider standards of membership, the question of foreign members, and to review the purposes of the Society.

Several weeks before the Washington meeting the following persons were appointed to serve on this committee: William Steere, Chairman; L. C. Dunn, Ernst Caspari, A. E. Mirsky, and Bruce Wallace. The committee made no formal report to the Society. However, individual members of the committee were consulted by members of the Executive Committee in regard to the purposes of the Society and standards of membership. The Secretary reported informally on the nature of these discussions and the recommendations which emerged from them. No action was taken on these remarks; the consensus of opinion held that a larger segment of the Society than that attending the business meeting should take part in deciding these matters.

Following these remarks the meeting adjourned.

Bruce Wallace, Secretary

REPORT OF THE TREASURER

Balance on hand August 15, 1957	$ 818.60
Income from dues August 15, 1957 to December 1, 1958	2746.55
TOTAL RECEIPTS	$3565.15
Expenditures August 15, 1957 to December 1, 1958	
L. C. Dunn, Editorial expenses	$ 300.00
506 subscriptions to The American Naturalist	1771.00
14 subscriptions to The American Naturalist	49.00
A.I.B.S. dues	486.00
A.I.B.S. invoice 1673, Secretarial expenses	8.73
Long Island Biological Association, Secretarial expenses	14.57
TOTAL EXPENSES	$2629.30
Balance on hand, College Savings Bank, Ames, Iowa, December 1	$ 935.85

G. F. Sprague, Treasurer

We, the undersigned have examined the Treasurer's books, bank deposits, etc., and find the record presented above to be correct.

Sterling B. Hendricks
Haig Dermen Auditors

REPORT OF THE EDITOR

August 1, 1957-December 31, 1958

During this period 85 manuscripts were received, including 23 letters to the editors. Of these eight were rejected, five as data papers on rather specialized problems, three as not meeting our scientific requirements.

In the 1958 volume we published 31 articles. Eleven of these dealt with some aspect of evolution, nine with problems of experimental genetics, and eight with development or metabolism. In addition we published 14 letters to the editors.

During the year at a time when the rate of receipt of manuscripts had declined, the editorial board agreed to a change in our system of priorities to permit publication of more data papers. No change in policy was involved and the rate of receipt of manuscripts is now such that we shall have to adhere to our policy of preference for papers of general theoretical interest.

Dr. Demerec kindly assumed the duties of the managing editor during his absence in July and August.

L. C. Dunn

THE AMERICAN NATURALIST

VOL. XCIII September-October, 1959 No. 872

RECORDS of the AMERICAN SOCIETY OF NATURALISTS

RECORDS V, PART 3

Issued as a Supplement to *The American Naturalist*,
Volume XCIII, No. 872

1959
Prepared by the Secretary
BRUCE WALLACE

Subscription, $8.00 a year, postpaid in the United States, $8.50 in Canada, $8.75 elsewhere. Special rates for students; apply to the publisher. Single copies may be purchased for $1.35 for issues of the current year and $2.00 for issues after 1939; $3.00 for earlier issues.

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820 College Avenue
Tempe, Arizona

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RECORDS

of the

AMERICAN SOCIETY OF NATURALISTS

Volume V
Part Three

EXECUTIVE COMMITTEE, 1959

Officers

	Years to Serve
Dr. Paul B. Sears, President *Dept. of Conservation, Yale University*	1959
Dr. Arthur D. Hasler, Vice-President *Dept. of Zoology, University of Wisconsin*	1959
Dr. Earl L. Green, Secretary *Jackson Laboratory, Bar Harbor, Maine*	1959–1961
Dr. George F. Sprague, Treasurer *FCD-ARS, Plant Industry Station, Beltsville, Md.*	1957–1959

Additional Members of the Executive Committee

Dr. G. Evelyn Hutchinson *Dept. of Zoology, Yale University*	1959–1961
Dr. William C. Steere *New York Botanical Garden*	1958–1960
Dr. E. Newton Harvey *Dept. of Biology, Princeton University*	1957–1959
Dr. Jack Schultz *Institute for Cancer Research, Fox Chase, Philadelphia*	1959

RECENT MEETINGS AND PRESIDENTS OF THE AMERICAN SOCIETY OF NATURALISTS*

	Date	*Location*	*President*
67.	1949, Dec. 29	New York	T. M. Sonneborn
68.	1950, Sept. 13	Columbus	Th. Dobzhansky
69.	1951, Sept. 12	Minneapolis	P. C. Mangelsdorf
70.	1952, Sept. 10	Ithaca	Sewall Wright
71.	1953, Dec. 28	Boston	L. J. Stadler
72.	1954, Sept. 7	Gainesville	M. Demerec
73.	1955, Sept. 7	East Lansing	K. V. Thimann
74.	1956, Aug. 29	Storrs	E. Newton Harvey
75.	1957, Aug. 28	Stanford	William C. Steere
76.	1958, Dec. 31	Washington, D. C.	G. Evelyn Hutchinson

RECENT VICE-PRESIDENTS†

K. V. Thimann, 1949
Harold H. Plough, 1950
B. P. Kaufmann, 1951
C. B. Van Niel, 1952
Alexander Hollaender, 1953
Ralph W. Chaney, 1954
E. G. Butler, 1955
Frank A. Brown, 1956
I. Michael Lerner, 1957
Jack Schultz, 1958

RECENT SECRETARIES†

Leon J. Cole, 1927–31
E. W. Lindstrom, 1932–34
A. M. Banta, 1935–37
Ralph E. Cleland, 1938–40
Alfred C. Kinsey, 1941–43
Wm. Randolph Taylor, 1944–46
W. S. Stone, 1947–49
Bentley Glass, 1950–52
Warren P. Spencer, 1953–55
Bruce Wallace, 1956–58

RECENT TREASURERS†

Edmund W. Sinnott, 1926–28
Sewall Wright, 1929–32
M. Demerec, 1933–35
R. A. Brink, 1936–38
H. H. Plough, 1939–41
W. R. Irwin, 1942–44
T. M. Sonneborn, 1945–47
D. P. Costello, 1948–50
D. F. Poulson, 1951–53
Carl P. Swanson, 1954–56

*A complete list of the first 76 meetings is given in these Records, Volume V, Part 2.

†Complete lists of these officers are to be found in these Records, Volume V, Part 2.

THE ORIGINAL CALL

The following is a copy of the original call for the first meeting, which was issued by Professor Samuel F. Clarke, of Williamstown, in March, 1883:

A number of American workers in Biology, desiring to have established an association of American naturalists for business purposes, extend to you a cordial invitation to join in a movement looking toward that end.

The intention is to have an annual meeting, for the purpose of discussing topics of common interest, for which, at present, no opportunity is afforded; as, for example, museum interests, in connection with which each museum director could indicate his plan of work, the special group of which he was making exhaustive collections, so that work may not be uselessly duplicated in many places; methods of museum work; methods of exhibition, etc.; methods of laboratory work; laboratory technique; new and valuable points in staining, mounting, cutting, and preserving of sections; systems of instruction in various departments of natural science; methods with small elective classes; with large college classes; the position which the observational sciences should hold in the college curriculum; the amount of natural science which should appear in college entrance examinations; the amount and character of such instruction in preparatory school, etc.

It is further believed that such a society could materially influence for the better the cause of science in America; that it would have a very healthful general effect, and could exert a strong influence in many directions where at present it seems to be very much needed. It is proposed to have the first meeting, which will be preliminary to organization, and, therefore, of prime importance, at Springfield, Mass., in the Springfield High School Hall, Friday, April 10.

The following gentlemen are interested in the enterprise, and nearly all of them will be among those present: [the names are J. M. Tyler, A. Hyatt, C. S. Minot, A. S. Packard, Jr., S. H. Scudder, H. N. Martin, W. T. Sedgwick, G. Macloskie, W. Libbey, H. F. Osborn, W. B. Scott, W. N. Rice, S. I. Smith, S. F. Clarke (secretary)].

THE CONSTITUTION

ARTICLE I

Name and Objects

Section 1. This association shall be known as the American Society of Naturalists.

Section 2. The object of this Society shall be the association of working naturalists for the discussion, advancement and diffusion of knowledge concerning the broader biological problems, including organic evolution, thus serving to correlate the various biological sciences into a common philosophy of biology.

ARTICLE II

Members

Section 1. Membership in the Society shall be limited to persons professionally engaged in some branch of natural history, as, instructors in natural history, officers of museums and other scientific institutions, physicians, and others, who have essentially promoted the natural history sciences by original contributions of any kind. Any member may present to the executive committee of the Society, through the secretary, names of candidates for membership and those candidates who are approved by the committee may be elected to membership in the Society by a majority of the members present at any meeting of the Society. The names of candidates not elected to membership within three years of the date of consideration shall be removed from the list of nominees unless renominated.

Section 2. Each active member shall pay to the treasurer of the Society annual dues of the amount provided in the By-Laws, and considered due on January first of each year. The name of any member two years in arrears for annual assessments shall be erased from the list of the Society, and such person can only regain membership by re-election.

Section 3. Honorary members, exempt from the payment of dues, may be elected upon the recommendation of the executive committee by a two-thirds vote of the members present at any meeting of the Society. The number of honorary members is limited to ten. Emeritus members, upon retirement from their professional posts, are exempt from dues.

ARTICLE III

Officers

Section 1. The officers of the Society shall be a president, a vice-president, a secretary and a treasurer. These, together with the three most recent past-presidents and the retiring vice-president, shall constitute the executive committee of the Society.

Section 2. The president and vice-president shall be elected for a term of one year, the secretary and treasurer for a term of three years. Each president on retirement shall serve on the executive committee for three years. Each vice-president and secretary on retirement shall serve on the executive committee for one year. The election of officers shall take place at the annual meeting of the Society, and their official terms shall begin on the following January first. They shall continue in office until new officers are installed. In case the annual meeting is postponed to a date subsequent to January first of the next year, the terms of the new officers shall begin immediately upon election.

Section 3. The officers named in Section 1 shall discharge the duties usually assigned to these respective officers. The executive committee shall recommend to the Society from time to time such measures as they may deem expedient for the purposes of the Society, besides discharging the specific duties assigned to them by this constitution.

Section 4. Vacancies in the board of officers, occurring by death, resignation, or otherwise, may be filled by election by ballot at any meeting of the Society. A vacancy in the secretaryship or treasurership occurring in the interval of the meetings of the Society may be filled by appointment by the executive committee; but the person so appointed shall hold office only until the next meeting of the Society.

ARTICLE IV

Meetings

Section 1. The annual meeting shall be held during convocation week, unless otherwise ordered by the executive committee.

Section 2. Special meetings may be appointed at any time by a vote of the Society or of the executive committee.

Section 3. Sections of the Society may be organized in any locality, with the approval of the Society in each case, by ten or more members for the purpose of holding meetings for the presentation of scientific papers. Such sections shall have the right to elect their own officers and associate members, but associate membership in any section shall not confer membership in the Society.

ARTICLE V

Quorum

Fifteen members shall constitute a quorum of the Society, and three a quorum of the executive committee.

ARTICLE VI

Accounts

A committee shall be appointed at each annual meeting to audit the accounts of the treasurer for the year closing with that meeting.

ARTICLE VII

Affiliated Societies

The Society may affiliate with other scientific organizations.

ARTICLE VIII

By-Laws

Section 1. By-laws recommended by the executive committee may be adopted at any meeting by a majority vote.

Section 2. By-laws may be repealed at any meeting upon recommendation of the executive committee, by a majority vote.

ARTICLE IX

Amendments

Amendments to the constitution, recommended by the executive committee, may be adopted at any annual meeting by a vote of two-thirds of the members present.

BY-LAWS

1. The programs shall be arranged by the vice-president in consultation with the president and the secretary.

2. Each president on retiring shall appoint a nominating committee of three members, including a chairman, for officers to be elected at the next annual meeting. The retiring president and the secretary shall be ex-officio members of this committee.

3. The executive committee shall be empowered to appoint an editor for *The American Naturalist*, to serve for a five-year term. The executive committee, in consultation with the editor, shall appoint an editorial board to advise the editor in matters of policy. Each member of the editorial board shall serve for a term of three years.

4. In return for $3.50 per individual subscription, the Science Press will provide an annual subscription to *The American Naturalist* for each active member not in arrears for dues; and also for each emeritus member who elects to subscribe for $3.50 per annum.

5. The Records of the Society shall be published once every three years beginning in 1914. The Records shall contain the constitution and by-laws of the Society, the minutes of all meetings held within the period covered, the treasurer's reports and a full list of members of the Society.

6. The Society shall reimburse the secretary for traveling and hotel expenses incurred in attending the annual meeting.

7. Active members shall pay dues of $5.00, which shall include a subscription to *The American Naturalist*. Emeritus members may receive the journal upon payment of $3.50 annually.

In the library of the Wistar Institute of Philadelphia will be found a complete set of the Records of the American Society of Naturalists together with printed announcements, programs, and reports, and also certain correspondence of historical interest. This matter, the property of the Society, is cared for through the courtesy of the Wistar Institute.

EDITOR'S NOTE: The Science Press is no longer responsible for the publication of *The American Naturalist*. Jaques Cattell, however, continues as publisher. Refer to By-Law No. 4.

Official Publications of the Society

RECORDS		
Volume I	Parts 1-12	1884-1895
Volume II	Parts 1-10	1896-1911
Volume III	Parts 1-6	1912-1931
Volume IV	Parts 1-6	1932-1949
Volume V	Part 1	1950-1952
Volume V	Part 2	1953-1955
Volume V	Part 3	1956-1958

MEMBERSHIP LIST

The date indicates the meeting at which the member was elected; thus 1929 denotes the meeting for the year 1929, although that meeting was actually held on January 1, 1930.

HONORARY MEMBERS

BEEBE, WILLIAM, Ph.D., *New York Zoological Park*, New York 60, N. Y. 1946.

HARRISON, ROSS G., Ph.D., Sc.D., LL.D., Professor Emeritus of Biology, Osborn Zoological Laboratory, *Yale University*, New Haven, Conn. 1893.

HOLMES, SAMUEL J., Ph.D., Professor Emeritus of Zoology, *University of California*, Berkeley 4, Calif. 1904.

MULLER, HERMANN J., Ph.D., D.Sc., Professor of Zoology, *Indiana University*, Bloomington, Ind. 1916.

PATTERSON, JOHN T., Ph.D., D.Sc. (hon.), Professor Emeritus of Zoology, *University of Texas*, Austin 12, Texas. 1919.

PAYNE, FERNANDUS, Ph.D., Sc.D. (hon.), LL.D., Professor Emeritus of Zoology, *Indiana University*, Bloomington, Ind. 1911.

PETRUNKEWITCH, ALEXANDER, Ph.D. Sc.D., Professor Emeritus of Zoology, *Yale University*, New Haven, Conn. 1910.

SHULL, A. FRANKLIN, Ph.D., Professor Emeritus of Zoology, *University of Michigan*, 431 Highland Road, Ann Arbor, Mich. 1911.

SMITH, GILBERT M., Ph.D., Sc.D., Professor Emeritus of Botany, *Stanford University*, Stanford, Calif. 1928.

WRIGHT, SEWALL, Sc.D., LL.D., L. J. Cole Professor of Genetics, *University of Wisconsin*, Madison 6, Wis. 1915.

EMERITUS MEMBERS

ACKERT, JAMES EDWARD, Ph.D., *Kansas State College*, Manhattan, Kan. 1931.

ADDISON, WILLIAM H. F., M.D., 286 East Sidney Avenue, Mount Vernon, N. Y. 1920.

ALLARD, H. A., 3000 7th Street North, Arlington, Va. 1931.

ALLEN, ARTHUR A., Ph.D., Dept. of Conservation, *Cornell University*, Ithaca, N. Y. 1934.

ANDREWS, ETHAN A., Ph.D., 107 East Lake Avenue, Baltimore 12, Md. 1888.

APPLEMAN, CHARLES O., Ph.D., *University of Maryland*, College Park, Md. 1925.

BAILEY, C. H., Ph.D., *University of Minnesota*, University Farm, St. Paul, Minn. 1933.

BAITSELL, GEORGE A., Ph.D., Professor of Biology, *Yale University*, Osborn Zoological Laboratory, New Haven, Conn. 1915.

BARSS, HOWARD P., S.M., 6129 S. W. 45th Avenue, Portland 19, Ore. 1936.

BARTLETT, HARLEY HARRIS, Dept. of Botany, *University of Michigan*, Ann Arbor, Mich. 1913.

BARTSCH, PAUL, Ph.D., Sc.D., Curator Mollusks and Cenozoic Invertebrates, U. S. National Museum, *Smithsonian Institution*, Washington, D. C. 1931.

BENNETT, JAMES P., Ph.D., 151 Hilgard Hall, *University of California*, Berkeley, Calif. 1943.

BIGELOW, HENRY B., Ph.D., Emeritus Professor of Zoology, *Harvard University*, Museum of Comparative Zoology, Cambridge 38, Mass. 1910.

BONIN, GERHARDT VON, M.D., Dept. of Anatomy, *University of Illinois*, College of Medicine, Chicago 12, Ill. 1947.

BORING, ALICE M., Ph.D., 44 Martin Street, Cambridge 38, Mass. 1911.

BRADLEY, JAMES C., Ph.D., Emeritus Professor of Entomology, *Cornell University*, Ithaca, N. Y. 1910.

BROWNE, WILLIAM W., Ph.D., Professor of Bacteriology, *College of City of New York*, 139th Street and Convent Avenue, New York, N. Y. 1914.

BUCHANAN, R. E., Ph.D., 503 Welch Avenue, Ames, Ia. 1932.

CALVERT, PHILIP P., Ph.D., Professor Emeritus of Zoology, *University of Pennsylvania*, P. O. Box 14, Cheyney, Pennsylvania. 1913.
CHAMBERLIN, RALPH V., Ph.D., Sc.D., Emeritus Professor of Zoology, *University of Utah*, Salt Lake City, Utah. 1914.
CHANDLER, W. H., Ph.D., Emeritus Professor of Horticulture, College of Agriculture, *University of California*, Berkeley, Calif. 1927.
COE, WESLEY R., Ph.D., *Scripps Institution of Oceanography*, La Jolla, Calif. 1893.
COKER, ROBERT E., Ph.D., Dept. of Zoology, *University of North Carolina*, Chapel Hill, N. C. 1929.
COLLINS, JULIUS L., Ph.D., R.D. 1, Box 369, Alpine, Calif. 1934.
COLTON, HAROLD S., Ph.D., Box 601, Flagstaff, Ariz. 1910.
CONARD, HENRY S., Ph.D., Lake Hamilton, Fla. 1932.
CONN, HAROLD J., Ph.D., 458 Castle Street, Geneva, N. Y. 1934.
COONS, GEORGE H., Ph.D., Division of Sugar Planting Investigation, BPI Station, Beltsville, Md. 1937.
COOPER, WILLIAM S., Ph.D., Sc.D., 1421 Bluebell Avenue, Boulder, Colo. 1936.
CORT, W. W., Ph.D., School of Public Health, *University of North Carolina*, Chapel Hill, N. C. 1924.
COWDRY, E. V., Ph.D., Wernse Covier Research Laboratory, *Washington University*, Medical School, St. Louis, Mo. 1925.
CURTIS, MAYNIE R., Ph.D., 2850 Cocoanut Avenue, Miami 33, Fla. 1914.
CURTIS, WINTERTON CONWAY, Ph.D., 210 Westmount Avenue, Columbia, Mo. 1904.

DANFORTH, CHARLES H., Ph.D., Sc.D., Emeritus Professor of Anatomy, Dept. of Anatomy, *Stanford University*, Calif. 1930.
DENNY, F. E., Ph.D., 1013 Locust St., N.E., St. Petersburg, Fla. 1932.
DODGE, BERNARD O., Ph.D., Emeritus Plant Pathologist, *New York Botanical Garden*, New York, N. Y. 1928.
DORSEY, MAXWELL J., Ph.D., 1502 S. Lincoln Avenue, Urbana, Ill. 1931.

EAMES, ARTHUR J., Ph.D., Emeritus Professor of Botany, New York State College of Agriculture, *Cornell University*, Ithaca, N. Y. 1922.
EDWARDS, DAYTON J., Ph.D., Emeritus Professor of Physiology, *Cornell Medical College*, 1300 York Avenue, New York, N. Y. 1914.
EHLERS, JOHN H., Ph.D., 1160 Holland Street, Lakewood, Colorado. 1936.
EVANS, ALEXANDER W., Ph.D., Emeritus Professor of Botany, *Yale University*, 180 Livingston Street, New Haven, Conn. 1893.
EYSTER, WILLIAM H., Ph.D., 235 Harrison St., Emmaus, Pa. 1932.

FAULL, JOSEPH H., Ph.D., 72 Fresh Pond Lane, Cambridge 38, Mass. 1929.
FIELD, WILLIAM L. W., A.M., *Milton Academy*, Milton, Mass. 1910.

GARBER, RALPH J., Ph.D., 613 West Park Avenue, State College, Pa. 1928.
GATES, WILLIAM H., Sc.D., R.D. 3, Perkins Road, Baton Rouge, La. 1932.
GEROULD, JOHN H., Ph.D., 36 Occom Ridge, Hanover, N. H. 1904.
GOLDFORB, A. J., Ph.D., Emeritus Professor of Biology, *College of City of New York*, Convent Avenue and 139th Street, New York 31, N. Y. 1910.
GOODALE, H. D., Ph.D., Biologist, Mount Hope Farm, 257 West Main Street, Williamstown, Mass. 1921.
GREGORY, WILLIAM K., Ph.D., Sc.D., Dept. of Ichthyology and Comparative Anatomy, *American Museum of Natural History*, 79th Street and Central Park West, New York 24, N. Y. 1917.
GUDGER, EUGENE W., Ph.D., *American Museum of Natural History*, 77th Street and Central Park West, New York 24, N. Y. 1925.
GULICK, ADDISON, Ph.D., 3 Concord Avenue, 562, Cambridge 38, Mass. 1946.
GUYER, MICHAEL F., Ph.D., 138 North Prospect Avenue, Madison, Wis. 1904.

HADLEY, PHILIP B., Ph.D., Camp Beavertail, Cedarville, Mich. 1922.
HAHN, CLARENCE W., M.S., 3314 Murray Lane, Flushing 4, N. Y. 1910.
HANKINS, FRANK H., Ph.D., 197 Elm Street, Northampton, Mass. 1936.
HARGITT, GEO. T., Ph.D., Sc.D., Dept. of Zoology, *Duke University*, Durham, N. C. 1932.

HARMAN, MARY T., Ph.D., Dept. of Zoology, *Kansas State College*, Manhattan, Kan. 1928.

HART, GEORGE H., V.M.D., M.D., *University of California*, School of Veterinary Medicine, Davis, Calif. 1934.

HARTMAN, CARL G., Ph.D., 219 Norwood Avenue, North Plainfield, N. J. 1924.

HAYES, HERBERT K., Sc.D., 1460 Hythe Street, St. Paul 8, Minn. 1911.

HERRICK, CHARLES J., Ph.D., Sc.D., 236 Morningside Drive, Grand Rapids, Mich. 1904.

HEUSER, CHESTER H., Ph.D., Dept. of Microscopic Anatomy, *Medical College of Georgia*, Augusta, Ga. 1915.

HUNT, HARRISON R., Ph.D., Dept. of Zoology, *Michigan State College*, East Lansing, Mich. 1931.

HUTCHISON, C. B., LL.D., College of Agriculture, *University of California*, Berkeley 4, Calif. 1931.

JACKSON, HARTLEY H. T., Ph.D., Room 61, U. S. National Museum, Washington 25, D. C. 1914.

JACOBS, MERKEL H., Ph.D., Emeritus Professor of General Physiology, Medical Laboratory, *University of Pennsylvania*, Philadelphia, Pa. 1913.

JOHANNSEN, OSKAR A., Ph.D., 203 Parkway, Ithaca, N. Y. 1923.

JORDAN, HARVEY E., Ph.D., Dept. of Medicine, Anatomy Pavilion VIII, East Lawn, *University of Virginia*, Charlottesville, Va. 1911.

KEPNER, WILLIAM A., Ph.D., 29 University Place, Charlottesville, Va. 1931.

KIESSELBACH, T. A., Ph.D., Emeritus Professor of Agronomy, Dept. of Agronomy, *University of Nebraska*, Lincoln, Nebr. 1932.

KILLIP, ELLSWORTH P., U. S. National Museum, Department of Botany, *Smithsonian Institution*, Washington 25, D. C. 1946.

KRAUS, E. J., Ph.D., Dept. of Botany, *Oregon State College*, Corvallis, Ore. 1927.

KUDO, RICHARD R., Sc.D., Institute of Microbiology, *Rutgers University*, New Brunswick, N. J. 1946.

KUNKEL, L. O., Ph.D., *Rockefeller Institute for Medical Research*, 66th Street and York Avenue, New York 31, N. Y. 1931.

LA RUE, GEORGE R., Ph.D., 7203 Wells Parkway, Hyattsville, Md. 1931.

LEWIS, IVEY F., Ph.D., 1110 Rugby Road, Charlottesville, Va. 1921.

LINK, GEORGE K. K., Ph.D., Dept. of Botany, *University of Chicago*, Chicago 37, Ill. 1931.

LOVE, HARRY H., Ph.D., 119 Oak Hill Road, Ithaca, N. Y. 1911.

MacDOWELL, EDWIN C., Sc.D., Dept. of Genetics, *Carnegie Institution of Washington*, Cold Spring Harbor, L. I., N. Y. 1916.

MACHT, D. I., M.D., Div. of Pharmacology, *Sinai Hospital Laboratory*, Baltimore 5, Md., 1929.

MATHESON, ROBERT, Ph.D., 204 Parkway, Ithaca, N. Y. 1935.

MAVOR, JAMES W., Ph.D., 8 Gracewood Park, Cambridge 38, Mass. 1927.

McATEE, WALDO L., A.M., 3 Davie Circle, Chapel Hill, N. C. 1931.

MEEK, WALTER J., Ph.D., 2015 Chadbourne Avenue, Madison 5, Wis. 1932.

MELANDER, AXEL L., Sc.D., 4670 Ladera Lane, Riverside, Calif. 1934.

MELHUS, I. E., Ph.D., 407 Pearson Avenue, Ames, Ia. 1931.

MOORE, BARRINGTON, M.F., 340 West 23rd Street, New York 11, N. Y. 1929.

MOORE, J. PERCY, Ph.D., Highland Avenue, Route 2, Media, Pa. 1913.

MORGAN, ANN H., Ph.D., Professor of Zoology, *Mount Holyoke College*, South Hadley, Mass. 1919.

MURNEEK, ANDREW E., Ph.D., Professor of Horticulture, *University of Missouri*, Columbia, Mo. 1936.

NABOURS, ROBERT K., Ph.D., Professor of Zoology, *Kansas State College*. Manhattan, Kan. 1917.

NEWMAN, HORATIO H., Ph.D., 173 Devon Drive, Clearwater, Fla. 1918.

NICE, LEONARD B., Ph.D., 5725 South Harper Avenue, Chicago 37, Ill. 1915.

OSTERHOUT, WINTHROP J. V., Ph.D., Emeritus Member, *Rockefeller Institute for Medical Research*, 66th Street and York Avenue, New York 21, N. Y. 1916.

PACKARD, CHARLES, Ph.D., *Marine Biological Laboratory*, Woods Hole, Mass. 1932.

PEARSE, ARTHUR S., Ph.D., Emeritus Professor of Zoology, *Duke University*, Durham, N. C. 1914.

PEEBLES, FLORENCE, Ph.D., 380 Rosemont Avenue, Pasadena 3, Calif. 1902.

POOL, RAYMOND J., Ph.D., 2845 South 27th Street, Lincoln 2, Nebr. 1931.

RAND, FREDERICK V., Ph.D., 10608 Nash Place, Kensington, Md. 1943.

RAND, HERBERT W., Ph.D., 7 Siders Pond Road, Falmouth, Mass. 1914.

RICE, EDWARD L., Ph.D., Sc.D., 2241 South Seneca Avenue, Alliance, Ohio. 1896.

RICHARDS, AUTE, Ph.D., 2950 East Mabel Street, Tucson, Ariz. 1913.

RIDDLE, OSCAR, Ph.D., LL.D., Route 4, Plant City, Fla. 1915.

ROBERTS, ELMER, Ph.D., Dept. of Animal Science, College of Agriculture, Urbana, Ill. 1931.

RUTHVEN, ALEXANDER G., Ph.D., Sc.D., *University of Michigan*, 3530 Rackham, Ann Arbor, Mich. 1916.

SATINA, SOPHIE, 45 East End Avenue, Apt. 5A, New York 28, N. Y. 1933.

SCHRAMM, JACOB R., Ph.D., 22 Macfarlane Hall of Botany, *University of Pennsylvania*, Philadelphia 4, Pa. 1919.

SCOTT, GEORGE G., Ph.D., 460 Henkel Circle, Winter Park, Fla. 1910.

SHAFER, GEORGE D., Ph.D., 321 Melville Avenue, Palo Alto, Calif. 1911.

SHARP, LESTER, Ph.D., Sc.D., Neuvo, Calif. 1922.

SHELFORD, VICTOR E., Ph.D., *University of Illinois Vivarium*, Wright and Healey Streets, Champaign, Ill. 1918.

SHERFF, EARL E., Ph.D., 1203 South Church Street, Hastings, Mich. 1946.

SHULL, CHARLES ALBERT, Ph.D., 42 Oakwood Road, Asheville, N. C. 1923.

SNODGRASS, ROBERT E., 3706 13th Street, N.W., Washington 10, D. C. 1935.

STAKMAN, ELVIN C., Ph.D., Div. of Plant Pathology, University Farm, St. Paul 8, Minn. 1921.

STARK, MARY B., Ph.D., Sc.D., Harris, Minn. 1919.

TASHIRO, SHIRO, Ph.D., Professor of Biochemistry, College of Medicine, *University of Cincinnati*, Cincinnati, Ohio. 1928.

TRANSEAU, EDGAR N., Ph.D., Dept. of Botany, *Ohio State University*, Columbus, Ohio. 1918.

TURNER, CLARENCE LESTER, Ph.D., Emeritus Professor of Zoology, Dept. of Biological Science, *Northwestern University*, Evanston, Ill. 1931.

VAN NAME, WILLARD G., Ph.D., *American Museum of Natural History*, 77th Street and Central Park West, New York, N. Y. 1899.

WAITE, FREDERICK C., Ph.D., 144 Locust Street, Dover, N. H. 1904.

WELCH, PAUL S., Ph.D., Dept. of Zoology, *University of Michigan*, Ann Arbor, Mich. 1934.

WELLS, BERTRAM W., Ph.D., Dept. of Botany, *State College*, Raleigh, N. C. 1942.

WENRICH, DAVID H., Ph.D., Dept. of Zoology, *University of Pennsylvania*, Philadelphia, Pa. 1916.

WENTWORTH, EDWARD N., M.S., Red Oak Ridge, R.D. 1, Box 73, Chesterton, Ind. 1911.

WHITE, ORLAND E., Sc.D., 1708 Jefferson Park Avenue, Charlottesville, Va. 1914.

WHITING, PHINEAS W., Ph.D., Dept. of Zoology, *University of Pennsylvania*, Philadelphia 4, Pa. 1913.

WHITNEY, DAVID D., Ph.D., Emeritus Professor of Zoology, *University of Nebraska*, Lincoln 8, Nebr. 1911.

WIEMAN, HARRY L., Ph.D., Box 485, Falmouth, Mass. 1913.

WRIGHT, ALBERT H., Ph.D., Dept. of Zoology, *Cornell University*, Ithaca, N. Y. 1925.

ACTIVE MEMBERS

ABELSON, PHILIP H., Ph.D., Geophysical Laboratory, *Carnegie Institution of Washington*, 2801 Upton St., N.W., Washington 8, D. C. 1958.

ADAMS, AMY ELIZABETH, Ph.D., Professor of Zoology, *Mount Holyoke College*, South Hadley, Mass. 1939.

ADOLPH, EDWARD FREDERICK, Ph.D., Professor of Physiology, School of Medicine and Dentistry, *University of Rochester*, Rochester 7, N. Y. 1933.

AIKMAN, JOHN M., Ph.D., Professor of Botany, *Iowa State College*, Ames, Ia. 1946.

ALBRECHT, WILLIAM A., Ph.D., Dept. of Soils, College of Agriculture, *University of Missouri*, Columbia, Mo. 1946.

ALEXANDER, MARY L., Ph.D., Biology Dept., *University of Texas, M. D. Anderson Cancer Hospital and Tumor Institute*, Texas Medical Center, Houston 25, Tex. 1955.

ALLARD, R. W., Ph.D., Dept. of Agronomy, *University of California*, Davis, Calif. 1954.

ALLEN, GORDON, Ph.D., *National Institutes of Health*, Bethesda 14, Md. 1957.

ALTENBURG, EDGAR, A.M., Ph.D., Professor of Biology, *Rice Institute*, Houston, Tex. 1931.

ANDERSON, BERTIL GOTTFRID, Ph.D., Dept. of Zoology, *Pennsylvania State University*, State College, Pa. 1942.

ANDERSON, ERNEST G., Ph.D., Professor of Genetics, *California Institute of Technology*, Pasadena, Calif. 1926.

ANDERSON, NORMAN G., Ph.D., Biology Division, *Oak Ridge National Laboratory*, Post Office Box P, Oak Ridge, Tenn. 1953.

ANDERSON, THOMAS F., Ph.D., Johnson Foundation, *University of Pennsylvania*, Philadelphia 4, Pa. 1951.

ARMSTRONG, PHILIP B., B.S., M.D., Professor of Anatomy, College of Medicine, *Syracuse University*, Syracuse, N. Y. 1942.

ARONSON, LESTER R., Dept. of Animal Behavior, *American Museum of Natural History*, New York 24, N. Y. 1948.

ATWOOD, K. C., Ph.D., M.D., School of Medicine, *University of Chicago*, Chicago 37, Ill. 1952.

AUSTIN, MARY L., Ph.D., Professor of Zoology, 7 Halowell House, *Wellesley College*, Wellesley 81, Mass. 1950.

AVERY, GEORGE S., JR., Ph.D., Director, *Brooklyn Botanic Garden*, 1000 Washington Avenue, Brooklyn, N. Y. 1937.

AXELROD, DANIEL I., Ph.D., Dept. of Geology, 405 Hilgard Avenue, *University of California*, Los Angeles 24, Calif. 1950.

BAKER, HORACE BURRINGTON, Ph.D., Professor of Zoology, *University of Pennsylvania*, Philadelphia 4, Pa. 1924.

BAKER, WILLIAM K., Ph.D., Dept. of Zoology, *University of Chicago*, Chicago 37, Ill. 1952.

BALDWIN, J. T., JR., Ph.D., Professor of Biology, *College of William and Mary*, Box 1588, Williamsburg, Va. 1955.

BALL, ERNEST, Ph.D., Dept. of Botany, *North Carolina State College*, Raleigh, N. C. 1955.

BANGHAM, RALPH V., Ph.D., Dept. of Biology, *College of Wooster*, Wooster, Ohio. 1953.

BATES, MARSTON, Ph.D., Dept. of Zoology, *University of Michigan*, Ann Arbor, Mich. 1951.

BEAMS, HAROLD W., Ph.D., Professor of Zoology, *State University of Iowa*, Iowa City, Ia. 1939.

BECKER, ELERY R., Sc.D., Professor of Zoology, *Iowa State College*, Ames, Ia. 1946.

BELL, A. EARL, Ph.D., Life Science Building, *Purdue University*, Lafayette, Ind. 1958.

BENSON, LYMAN, Ph.D., Dept. of Botany, *Pomona College*, Claremont, Calif. 1955.

BERGER, CHARLES A., Ph.D., Dept. of Biology, *Fordham University*, New York 58, N. Y. 1943.

BERGNER, A. DOROTHY, Ph.D., Cytogeneticist, 3204 North Calvert Street, Baltimore 18, Md. 1933.

BERRY, L. JOE, Ph.D., Dept. of Biology, *Bryn Mawr College*, Bryn Mawr, Pa. 1954.

BERTALANFFY, LUDWIG VON, Ph.D., *The Menninger Foundation*, Topeka, Kans. 1953.

BILLINGS, W. D., Ph.D., Dept. of Botany, *Duke University*, Durham, N. C. 1955.

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1951—Minneapolis. *Patterns of Cellular Organization.*
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1951—Philadelphia. *Use of Statistical Models to Interpret Data on Human Population Genetics*
C. C. Li, J. V. Neel, Bentley Glass, J. N. Spuhler and D. J. Hager, Howard Levene

1952—Ithaca. *Biochemical Evolution*
Harold F. Blum, Urless N. Lanham, Sam Granick, Marcel Florkin.

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Alan D. Conger; E. B. Lewis; George H. Mickey; Robert Carter, V. P. Bond, James T. Brennan, and E. P. Cronkite; William L. Russell

1954—Gainesville. *The Origin of the Biota of Middle America*
Aaron J. Sharp; Paul S. Martin; Pierce Brodkorb; Coleman J. Goin

1955—East Lansing. *Modern Approaches to Problems of Differentiation*
Tracy M. Sonneborn; John P. Trinkaus; Armin C. Braun; William P. Jacobs

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Frank A. Brown; G. C. Stephens; C. S. Pittendrigh and Victor Bruce; G. E. Folk; M. Fingerman

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Meeting	*Date*	*Place*	*President*
65th	Dec. 29, 1949	New York	T. M. Sonneborn
	Heredity, Environment, and Politics		
66th	Sept. 13, 1950	Columbus	Th. Dobzhansky
	Evolutionary Changes in Mendelian Populations		
67th	Sept. 11, 1951	Minneapolis	Paul C. Mangelsdorf
	Evolution under Domestication		
68th	Sept. 9, 1952	Ithaca	Sewall Wright
	Gene and Organism		
69th	Dec. 30, 1953	Boston	L. J. Stadler
	The Gene		
70th	Sept. 7, 1954	Gainesville	M. Demerec
	What is a Gene?—Twenty Years Later		
71st	Sept. 7, 1955	East Lansing	K. V. Thimann
	Promotion and Inhibition: Twin Themes of Physiology		
72nd	Aug. 28, 1956	Storrs	E. Newton Harvey
	Evolution of Bioluminescence		
73rd	Aug. 27, 1957	Stanford	William C. Steere
	Evolution and Speciation in Mosses		
74th	Dec. 30, 1958	Washington, D. C.	G. Evelyn Hutchinson
	Homage to Santa Rosalia or *Why Are There So Many Different Kinds of Animals?*